EFFECTS OF WIND ON THE GROWTH AND PRODUCTIVITY OF GRASSES WITH SPECIAL REFERENCE TO TALL FESCUE (*FESTUCA ARUNDINACEA* SCHREB.)

J. R. THOMPSON

Doctor of Philosophy

Department of Forestry and Natural Resources

University of Edinburgh

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ABSTRACT

This study was set in the practical context of whether protection from wind by shelterbelts or windbreaks might increase the production of grasses in early spring.

Two field experiments were carried out in spring, 1970 at locations near Edinburgh. One experiment examined the effect of an artificial windbreak on the growth of S.170 Festuca arundinacea and S.24 Lolium perenne in relation to the direction of shelter and the supply of nutrients. The other experiment was concerned solely with a natural shelterbelt and the directional effects on the two species. Whilst both experiments were inconclusive, there were indications that shelter, especially from east or west, enhanced the early growth of both species, but only when nutrient supplies were adequate. This suggested that further experimentation under controlled conditions was required.

The controlled environment wind tunnel allowed conditions in spring in eastern Scotland to be simulated realistically. This instrument and the various modifications to the air flow, in the working section for experimental purposes, are described in detail.

A series of 4 experiments was carried out to examine the effects of wind on S.170 F. arundinacea. These experiments were factorially designed and incorporated 2 levels of nitrogen (21 and 621 p.p.m.), 2 levels of phosphorus (5-10 and 45 p.p.m.) and 2 levels of wind (0.6 and 3.5m s^{-1}). During growth in the wind tunnel, tillers were counted weekly and each experiment then terminated by a destructive harvest. The results of the final harvests reflected the trends shown in the tiller counts.

Two experiments were of special interest, since they also provided a means by which 2 levels of turbulence could be compared. In both experiments, wind was found to reduce substantially the yield of S.170

F. arundinacea, but only where nutrient supplies were adequate. The statistically significant responses were usually confined to the high nitrogen and high phosphorus treatment alone.

In both experiments, the effects of phosphorus and especially nitrogen were generally greater than wind.

In the low turbulence experiment (yield experiment 1), at high levels of nitrogen and phosphorus, wind reduced overall production by 20% and that of shoots by 20%, but had no significant effect on roots or the root:shoot ratio. The dry weights of live leaves were reduced by 24%, the remaining leaf sheaths and stems by 17%, the leaf length per plant by 38%, the number of leaves per plant by 23% and the number of tillers per plant by 18%. Although certain other parameters were also reduced on a per-tiller basis, the effect on the number of tillers was considered to be the main means by which the yields were reduced.

In a second experiment (yield experiment 4), the level of turbulence was increased to create greater leaf flutter. The reductions in yield, due to wind, were less pronounced, but it was considered that, because of exponential growth, the decrease in effect could not, with certainty, be attributed to increases in the level of turbulence.

In this experiment, at high levels of nitrogen and phosphorus, wind decreased overall production by 7%, but this effect was not significant. The yield of shoots was reduced by 12% and there was no significant effect on roots or the root:shoot ratio. The effect on leaf sheaths and stems was not significant, but there were significant reductions of 16% in the dry weight of live leaves, 17% in leaf area, 18% in the number of leaves and 13% in the number of tillers per plant. The individual tiller dry weight was not significantly affected by wind. A number of parameters also showed significant effects of wind in the low phosphorus, high nitrogen treatment.

In investigations of the reasons why the differences in yield were obtained, it was found that there was an after-effect on photosynthesis and transpiration. Net photosynthesis and leaf resistance were both reduced.

One possible reason for this was mechanical damage, resulting from leaf movement in the wind. This took the form of increased numbers both of transverse fold lines and also of abrasions on the leaf surfaces. The first type was assessed by counting and the second by examination under a stereoscan electron microscope. This showed the substantial damage that can occur to the leaf surface, as a result of contacts with other leaves; epicuticular waxes may be abraded and, in extreme cases, the epidermal cells torn open. It was considered that this damage could have contributed to water deficits in the leaves through a lowering of the cuticular diffusion resistance. This may have contributed to the reduced rates of photosynthesis with subsequent effects on the production of tillers and overall yields.

From the agricultural viewpoint, it was considered that the reduction of wind would be expected to increase production in spring, providing that growth was not limited by the availability of nutrients. The interaction with nutrients may explain why some of the investigations on shelter have been inconclusive and also suggests a means by which an increase in the effectiveness of fertilizers may be obtained.

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INTRODUCTION

CHAPTER 1.

INTRODUCTION

The title of this thesis, "Effects of wind on the growth and productivity of grasses with special reference to tall fescue Festuca arundinacea Schreb.", reflects the salient features of a programme of research supported by a grant to Dr. J. M. Caborn from the Department of Agriculture and Fisheries for Scotland. This grant was entitled "An investigation of shelter effects on the growth of pasture" and, although a broad title, it was understood that emphasis would be placed on a study of the factors affecting the resumption of grass growth in early spring.

This aspect is of particular relevance to farming on marginal land where the dominant grazing animal is the sheep. The production of lambs in spring at a time when the standing grass crop from the previous season has largely been depleted and when replenishment by early growth is of negligible proportions presents the farmer with a period of particular difficulty. Whilst vigilant attention by the shepherd to the needs of the lamb is essential, much depends on the quantity and quality of the fodder available to the ewe. Clearly, an increase in pasture production in early spring would be of considerable value and it has been suggested (Alcock, 1969; Caborn, 1971; Grant and King, 1969) that shelter might provide a means by which this could be achieved.

The beneficial effects of shelterbelts in ameliorating the climate of a grazing animal in winter have been widely accepted by farmers. This probably stems from the noticeable tendency of animals to seek shelter in periods of inclement weather. Although believed with quasi-religious fervour by a minority, it is fair to say that

there is far less acceptance by farmers of the value of shelter in increasing early crop production. There is evidence to suggest that advantageous tax concessions are often a more powerful incentive for the establishment of shelterbelts. Certainly few farmers would question the value of early bite, but many would question whether the provision of shelter, if of value at all, is the most effective means of achieving it. In fact there are several alternative strategies available.

One approach, perhaps of increasing relevance in view of the change towards later springs which seems to be taking place in the British climate (Lamb, 1965), would be to intensify the management of pastures in summer with a view to increasing the production of hay. By the installation of extra storage capacity, an insurance against the shortage of fodder in spring would be provided.

Plant breeders have recently directed much research effort towards the production of earlier strains of the main forage species, extensive use being made of mediterranean ecotypes. These efforts have achieved some success but in the cooler parts of Britain, there is often a dangerof extensive winter kill (Aldrich, 1969).

Agronomists have attempted to increase spring and autumn production by experimenting with management techniques such as frequency of cutting and rates of fertilizer application. Heavy application of nitrogen may well increase production but again with the attendant risk of winter kill.

One attractive approach has been to explore the potential for early production of some of the less widely used species. Tall fescue has been found to be particularly successful but has not gained widespread acceptance apparently because of difficulties in

establishment of the sward.

A strong impetus to the further exploration of the possible benefits of shelter comes from studies on horticultural crops where the value of shelter has far wider acceptance. Indeed the spectacular increases in yields of some crops, particularly raspberries and strawberries (Waister, 1970 and 1972a),is ample justification for further experimental investigation of the role of shelter in early production and also of the role of wind in affecting the yields of crops. Such crops are of high commercial value and this raises another issue which is crucial in determining whether a farmer is likely to plant shelterbelts: the outlay on shelterbelt installation in relation to the economic value of the crop. A small percentage increase in the yield of horticultural crops may produce a considerable increase in profits whereas an arable or grass crop would require much larger increases in order to ensure the same returns on capital expenditure. In the case of early bite, there is some similarity to the horticultural situation since the economic returns are certainly much higher for a given yield increase than they would be in summer when upland pastures in particular tend to be undergrazed. Thus,smaller increases in biological yield might still be of economic value.

The literature on the effects of shelter on grass production has been adequately covered in several reviewsin recent years (Jensen, 1954; Caborn, 1957; Van Eimern et al, 1964; Marshall, 1967). As this thesis is more concerned with wind, it was considered that a further review of shelter effects would be in-appropriate. Marshall, of whose work this thesis is,in some ways,an extension, concluded that "the use of shelter in Britain to increase yields of agricul-

tural crops may have only limited potential". He also noted the paucity of information about the effect of shelter on grasslands and also that much of the yield data was of little significance in the causal interpretation of the effects of shelter on growth.

In approaching a research problem of this nature, one which is wide in scope and of potential practical significance, the establishment of priorities with respect to field and laboratory experiments and an appropriate balance between them can be very important. Whilst there may be value in interpreting the results of field experiments in terms of laboratory results already obtained, it is likely to be more fruitful to transport a problem into laboratory having gained some insight into the more relevant factors from field observation. In the first approach there is a danger of a very biased interpretation of field results from laboratory experiments whose conception must be intuitive. Thus field experiments appeared to be the logical starting point in this programme.

The strategy adopted was to investigate initially by means of small-scale field experiements, whether shelter could affect grass growth in early spring. In this event, it was then planned to use the controlled environment wind tunnel to evaluate the extent to which wind might have been the main causal factor. If wind were also to affect yields in a similar manner, not only would this help to confirm the results of the shelter experiments, but would also provide a rational basis for investigating the mechanisms of wind action. Ultimately, this approach would be expected to lead to more fundamental physiological studies. It will be seen in the following chapters that it was possible to follow this strategy quite closely.

SECTION 2.

FIELD EXPERIMENTS

CHAPTER 2.

FIELD EXPERIMENTS - GENERAL APPROACHES

2.1 Introduction

In deciding on questions to ask in the field experiments, particular consideration was given to points arising from the previous work of Dr. J. K. Marshall in the Department of Forestry and Natural Resources.

In experiments with Brassica napus (swede) and Beta vulgaris (sugar beets), Marshall (1974) found that the growth rates in both the sheltered crops were initially higher than in the unsheltered controls. This caused production differences to diverge for the first part of the growing season after which a convergence occurred associated with the earlier attainment of the optimum leaf area index by the sheltered plants. Consequently, the final yields were not significantly different. This result is interesting as any "early bite" effect obtained from sheltering pastures would also be a reflection of an early divergence in growth rates between sheltered and unsheltered plants. Whether a convergence would occur later is of little interest since this would coincide with the summer period of high production when pastures are usually under-grazed rather than over-grazed.

In general, larger responses to shelter have been reported during drier than average years (van Eimern et al., 1964). However, in Marshall's experiments the growing seasons were cooler and wetter than average suggesting that his results may under-estimate the responses likely in normal years. In areas with variable climates, experiments on shelter should really continue over several seasons but, as the main concern of this thesis was the effects of wind, the

field experiments were restricted to one season only.

In addition to the variation between seasons, there may also be considerable variation in wind direction within a growing season. This aspect has been stressed by Caborn (1971) who pointed out that in eastern Scotland where winds are variable in direction, the reductions in windspeed actually achieved by a shelterbelt or windbreak during a whole growing season may be surprisingly low. In Marshall's experiments, the reductions in windspeed at 3h east of the windbreak were 22.7% in 1965 and 27.6% in 1966. At a distance of 9h the respective reductions were only 16.1% and 11.3%.

Unfortunately this means of assessment may overlook periods when plants are especially sensitive to wind; in such periods shelter may be highly beneficial and of lasting value. In the absence of data on any possible lasting effects of wind, it would be unwise to discount the possible advantages to be gained by shelter from the occasional severe exposure even though this might be but a fraction of the total run of wind in a growing season. Thus, where wind direction is variable, the alignment of shelterbelts and windbreaks may be important. This would be especially true of areas such as eastern Scotland where winds from certain directions are also associated with certain types of weather. It was therefore decided that provision should be made in the field experiments to assess the effects of direction of shelter.

The response of different species to shelter is another factor which may also vary. Marshall (1974) concluded that temperature was probably the main factor in the divergence of the swede yields but in sugar beets this effect was more likely to have been due to water stress. Also Waister (1970 and 1972a) has shown differences in

response to shelter between strawberries and raspberries. By the use of 2 species it was hoped to obtain some idea of the likely extent of such differences in grasses.

A further consideration was the possible interaction between responses to shelter and the availability of nutrients. Arable and horticultural crops tend to be grown on more fertile soils whereas in upland or marginal conditions, nutrients may be limiting. In a situation with limiting nutrient factors, the response to shelter may vary depending on which factor is limiting and by how much. Thus it was considered necessary to incorporate some variation in nutrient supply into the experiments.

Shelter may be provided in a variety of ways but, for farmers, the choice would usually be between an artificial windbreak and a shelterbelt. This was taken into account by having two experiments, one carried out on a site where an artificial windbreak could be erected and the other in the vicinity of an already existing shelterbelt.

The two field experiments were therefore designed to incorporate two sites, two species, shelter from different directions and variation in nutrient availability.

2.2 Selection of species

The two species selected for this experimental programme were S.24 Lolium perenne (perennial ryegrass) and S.170 Festuca arundinacea (tall fescue).

S.24 is very widely used in Scotland, England and Wales. In 1968 it was rated as the earliest yielding variety of ryegrass and clearly such a feature would be of advantage for early bite (N.I.A.B., 1968/69).In certain winters, particularly 1962/63 and

1968/69, it did however suffer severely from winter kill (Aldrich, 1969; Copeman, 1969). From the experimental viewpoint it is a more convenient variety than S.23 L.perenne on account of its somewhat reduced tillering capacity.

S.170 is not a widely used grass and yet it does have some outstanding qualities. In 1968, F. arundinacea accounted for only 0.5% of the total grass seed use in England and Wales and S.170 was only one of the four varieties then available. It is, however, one of the earliest grasses to grow in the spring as well as being drought resistant, winter hardy and persistent (N.I.A.B., 1968/69). It produces more dry weight of herbage during winter than most other grasses in Britain and certain North African ecotypes can produce about five times more harvestable dry matter in winter than S.170 (Robson, 1965 and 1967). The potential of S.170 as a source of early spring growth seems excellent, which suggests that this variety, combined with shelter, could make a powerful contribution to alleviating the problem of "early bite". The use of the North African ecotypes of F. arundinacea compared with S.170 has been extensively investigated (Robson, 1967 and 1968; Robson and Jewiss, 1968a and 1968b), again with the view to obtaining enhanced growth in early spring. Whilst these ecotypes may produce more dry matter in winter they are also less winter hardy, thus reflecting a similar pattern to the ryegrasses.

2.3 Selection of experimental sites

As the Department of Forestry and Natural Resources had no land at its disposal for such experiments, it was necessary to negotiate with local farmers before establishing experimental sites. Two such sites were selected, one nearby at Liberton where an artificial wind-

break could be erected and the other in the Lammermuir Hills where shelter was already provided by a belt of trees.

The site at Liberton (Grid Reference NT 262698) was on Tower Mains Farm, permission for its use having been kindly granted by its owner, Mr. R. Jacks. Located on a hillside sloping gently to the northeast, this site was particularly exposed to winds from the southwest descending with little topographic hindrance from the nearby Braid Hills. Fortunately the previous crop had been spring barley under-sown with Italian ryegrass which, at the time of the experiments, gave a fairly dense ground cover thus assuring any introduced experimental material an adequate 'fetch'. This term is used to denote the extent of surroundings with reasonably uniform surface characteristics. Because of its proximity to the Department of Forestry and Natural Resources, this site was chosen for the more intensive experimental work and environmental monitoring.

The site in the Lammermuir Hills (Grid Reference NT 634647) was chosen as being fairly typical of conditions in the Scottish Southern Uplands where sheep and cattle farming is practised. Superimposed on a landscape of rolling grouse moors is a network of shelterbelts some of which are derelict and most of which are of dubious value in providing shelter owing to the lack of branches close to the ground. In addition, there are a number of rectangular wooded areas probably planted with the original intention of providing cover for game. These areas, despite their low standard as shelterbelts, are widely used by sheep presumably for overhead shelter and the experimental site chosen typified such an area.

Permission to use the land was kindly granted by the owner, the late Mr. W. Sharp, a local sheep farmer. The site itself was on a

south facing hillside adjoining the B.6355 road and had an average elevation of 305 m. Protection from northerly winds was afforded topographically since above the belt the land rose to 344 m, the summit of Kingside Hill. The belt itself consisted of a mixture of Scots pine and larch, about 70 years of age and averaging 15 m in height. Although originally enclosed by a stone wall, only a remnant remained and the trees, mostly bare up to the crowns, were clearly of much diminished value as shelter.

The vegetation of the area was a typical Agrostis tenuis and Festuca ovina grassland giving way to Holcus mollis in the belt itself. Pteridium aquilinum was invading on both eastern and western sides whilst to the north, reflecting decreasing grazing pressure and probably more severe conditions, Nardus stricta gradually assumed dominance.

2.4 Experimental procedures

Whilst the objectives of the two field experiments were somewhat different, there were many aspects especially in the early stages, where the procedures used were identical.

Because experiments with shelter inevitably involve the use of fairly large areas of land, the danger of differences in shelter being confounded with soil differences is a very real one and this has frequently been pointed out (van Eimern et al, 1964). This difficulty can be obviated by increased replication but this may create problems in itself especially if space is limited. In these experiments it was decided to grow plants in boxes containing a rooting medium of known characteristics and transport the boxes to the field. There may be a problem in applying such results to natural field situations but

this was judged to be of less importance than the advantage of control over nutrient status. In any case, the main value of this type of experiment is in providing insight into the relative importance of the various factors affecting yield.

Consideration was given to the types of artificial soil mixes available and the University of California System (Matkin and Chandler, 1957) then adopted. These mixes consist of varied ratios of peat and sand to which may be added different levels of nutrients. The peat used was a standard sphagnum type but the sand, from the River Tay, was unfortunately coarser than that recommended but the only available at the time. The mix adopted corresponded closely to the type 11 c, one with peat and sand in equal proportions and the following amounts of nutrients were added per 1000l of mix:

Potassium nitrate	148 g
Potassium sulphate	148 g
Superphosphate	1480 g
Dolomite lime	4446 g
Calcium carbonate lime	1480 g
Hoof and Horn	1480 g

Boxes, 43 cm x 28 cm x 15 cm deep, were then filled with this mixture to a height of 1.5 cms from the rim of the box, watered and allowed to stand for about two weeks before seedlings were planted. These boxes were specially constructed as units to fit into the floor of the working section of a wind tunnel to provide blocks of vegetation for wind studies if so required. Made of 19 gauge galvanized iron, they were painted with three coats of polyurethane varnish both internally and externally to obviate any difficulties with zinc toxicity.

The seed of both species was supplied by the National Seed Development Organization. A germination test was carried out using a 1:1 peat:sand mix with added nutrients and, after twenty-eight days, this gave values of 91% for S.24 and 83% for S.170.

In establishing the swards in the boxes it was decided to first germinate the seeds and then transplant the seedlings to pre-selected sites in the boxes. This approach had the advantage of ensuring an equal spacing of the seedlings, thereby promoting more even growth and reducing variability. Each species was sown on 18.12.1969 in a shallow tray containing a 1:1 peat:sand mix with no added nutrients. The medium was sprinkled lightly with seeds which were then covered with a minimal depth of sand and watered regularly until the seedlings were large enough to transplant. One difficulty with this method is the check to growth which may occur with transplanting; it was found that by carefully judging the size of the plants, very high success rates could be obtained. Transplanting early gave the highest success rates but, at the same time, implied selection of those plants with the fastest emergence times, plants which might also have been atypical of the population in other respects. In transplanting, care was taken not to select systematically; plants were only rejected if they were albinos, obviously deformed, or if they were derived from double embryos.

Each box was planted with both species in 2 monoculture blocks of 24 individuals separated by a gap of 7.5 cm. Within each block the plants were arranged in a 5 cm square pattern in 4 rows of 6 plants. Peripheral plants in each block were respectively 1 cm from the sides and 3 cm from the ends of the box. For purposes of reducing edge effects, an arrangement of 4 rows of 6 plants left a central block of 8 plants to be used for precise measurements. At the time of

transplanting, the seedlings were generally 5 cm high and, in S.24, the second leaf was just emerging. The plants of S.170 had one leaf only and a less developed root system. To avoid damage to the roots, the plants were placed in holes 3 cm deep laid out by means of a grid.

After the treatments had been assigned, the boxes were left in the greenhouse at a temperature of about 20°C and during this period were randomised at weekly intervals. When the plants had reached a suitable size, they were moved to cold frames for initial hardening off and then to the outside. At this stage the plants were clipped to 8 cm to simulate a light grazing and additional nutrients added where appropriate. The boxes were then transported to the experimental sites.

2.5 Weekly tiller counts

The only index of growth whilst the plants were in the field was the number of tillers. These were counted initially and then at weekly intervals in both experiments once the boxes had been placed in their correct positions. Only the central 8 plants in each species block were used for counting. The initial counts, that on 14.4.1970 in the Liberton experiment and the final harvests included all 8 plants in the block; otherwise counts were confined to 5 plants selected at random.

Counting tillers, especially when small, is rather subjective and any less than 2 cm long were excluded. In S.170 new tillers tend to remain enclosed in the leaf sheaths until quite large. In such situations a tiller was always counted once it had emerged from the sheath even though the visible portion might have been very small. When technical assistance was available for counting, care was taken to ensure that estimates of tiller numbers were not affected. During

the course of the experiments differences in the rate of production of the 2 species quickly became apparent. S.24 produced many more tillers although the actual size of an individual tiller was much less. After the experiments had progressed several weeks, it was clear that to have counted accurately all tillers in S.24 would have entailed a major disturbance of the canopy, perhaps with damage to the plants themselves. Further counting was then abandoned until the final harvest. In S.170, the smaller number of tillers allowed counting to continue for the duration of the experiments.

2.6 Final harvest procedure

After transporting back to the laboratory, the boxes were all watered heavily to allow the plants to recover turgidity. After this, all plants were clipped just below the soil surface so that all the aerial parts were removed intact. The plants were then carefully washed and any adhering roots clipped off.

With S.170 the central eight plants in each group within the boxes were individually divided up into live leaves, dead leaves and the remaining leaf sheaths and stems. As before, any tillers under 2 cm in length were not recorded. Each fraction was then dried to constant weight in a forced air drying oven at 80^{o} before weighing.

With S.24 the same approach was originally adopted but was abandoned because of the time required to divide and count the various components, there being many more tillers and leaves than in S.170. Instead the number of tillers was recorded and then the whole plant placed in an oven to obtain its dry weight.

In both species the border plants round each block of eight central plants were also harvested and any adhering soil and roots removed. This material was then dried, ground and later analysed for

total nitrogen and total phosphorus contents.

2.7 Evaluation of results and conclusions

The results of the two field experiments comprised the weekly tiller counts, the measurements taken during the final harvests, the nutrient analyses and the micrometeorological data. Since only the weekly tiller counts were common to both experiments, all the results are considered in the separate chapters on each experiment.

The conclusions from these experiments and their significance for the wind tunnel studies are considered in Chapter 5.

CHAPTER 3.

LIBERTON FIELD EXPERIMENT

3.1 Introduction

This experiment, by far the larger of the two field experiments, was concerned with the effects of shelter produced by artificial windbreaks. In selecting an experimental design the following questions arising from Chapter 2 were considered:

1. How does shelter affect the early spring growth of S.24 *Lolium perenne* and S.170 *Festuca arundinacea* ?
2. How is this influenced by the direction of shelter ?
3. How is this influenced by the availability of two important nutrients, nitrogen and phosphorus ?
4. What are the microclimatological differences produced by shelter and to what extent can they be related to differences in plant growth ?

3.2 Experimental design

One difficulty which often arises in designing experiments which ask several questions simultaneously is the logistics involved. Compromises are often necessary and in this case a reduction in the number of replicates rather than treatments was chosen because of the need to take a wide look at the field situation in one growing season. The design chosen was factorial with 2 species, 5 levels of shelter, 2 levels of nitrogen, 2 levels of phosphorus and 2 replicates.

Caborn (1957) has shown that the main effect of a windbreak is experienced leeward rather than windward. Thus, by the use of 2 windbreaks, one orientated north-south and the other east-west, shelter from 4 directions was obtained. A nearby fully exposed area completed the 5 levels of shelter. Each windbreak was 12.2 m long and 1.2 m high. Mutual interference was avoided by siting the windbreaks 22.5 h apart since it is normally assumed that 20 h is the limit of effective leeward shelter. The layout of the experimental area is shown in Figure 3.1.

The windbreaks themselves consisted of polypropylene netting of 63% permeability which was pre-stretched before use and then supported by wire at the top and bottom. Five wooden posts provided the structural support against the wind.

At each position maximum shelter was ensured by placing the boxes close to the center of the windbreaks; 2 h distant for replicate 1 and 3 h distant for replicate 2. In addition to 8 boxes of grass, each position also had 2 rain gauges, 1 thermohygrograph and 1 anemometer. The arrangement of the boxes and instruments at a typical position is shown in Figure 3.2.

For convenience, the sheltered positions will be referred to as north, south, east and west, these being the wind directions to which each was fully exposed. The control position with no shelter will be referred to as exposed. The two levels of nitrogen will be referred to as N_1 and N_2 and phosphorus as P_1 and P_2.

3.3 Microclimatological measurements

One of the objectives of this experiment was to relate any differences in grass growth to the microclimatological changes induced

FIGURE 3.1 LIBERTON FIELD EXPERIMENT GRID REFERENCE NT 262698

LAYOUT OF EXPERIMENTAL SITE

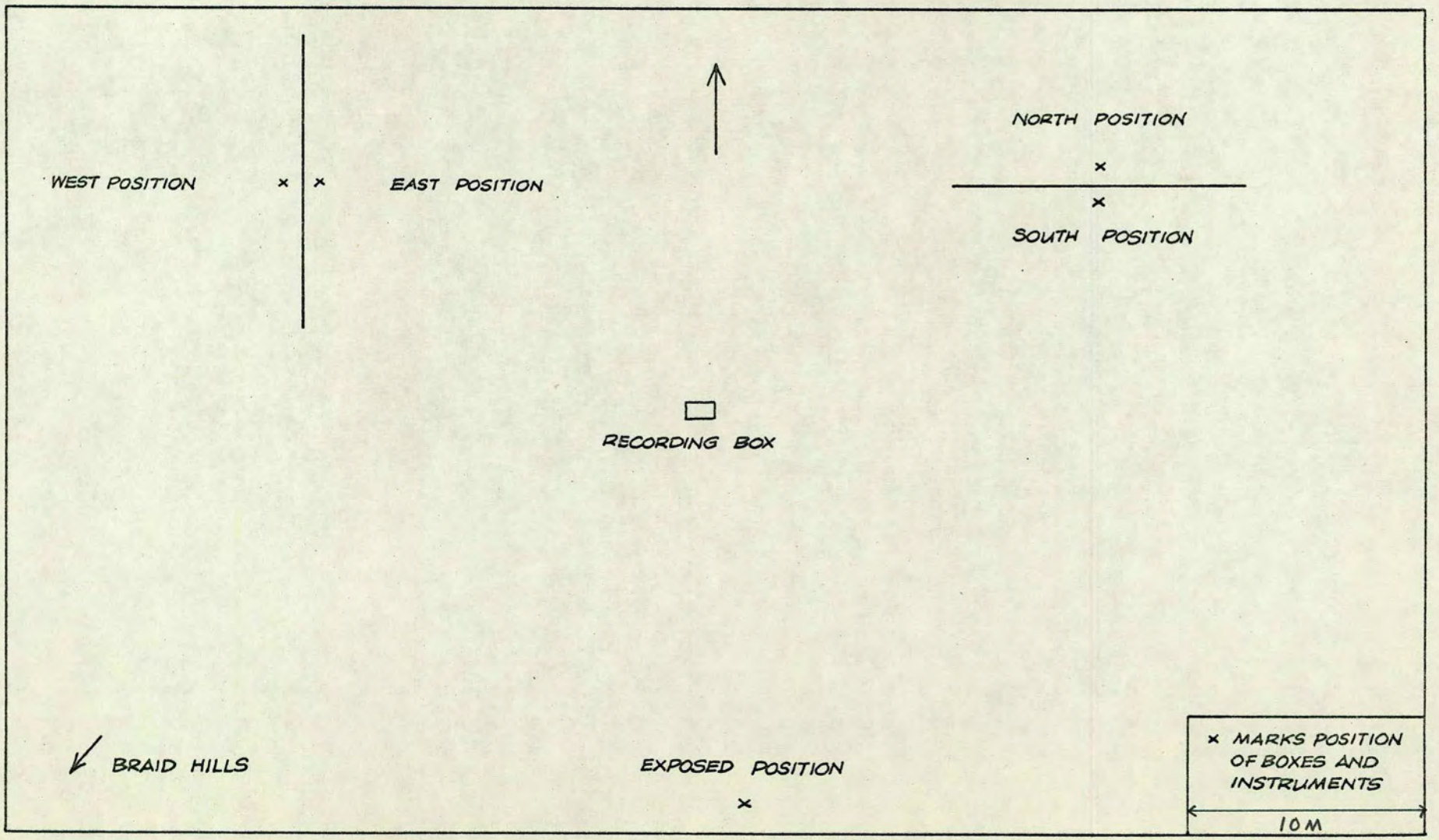
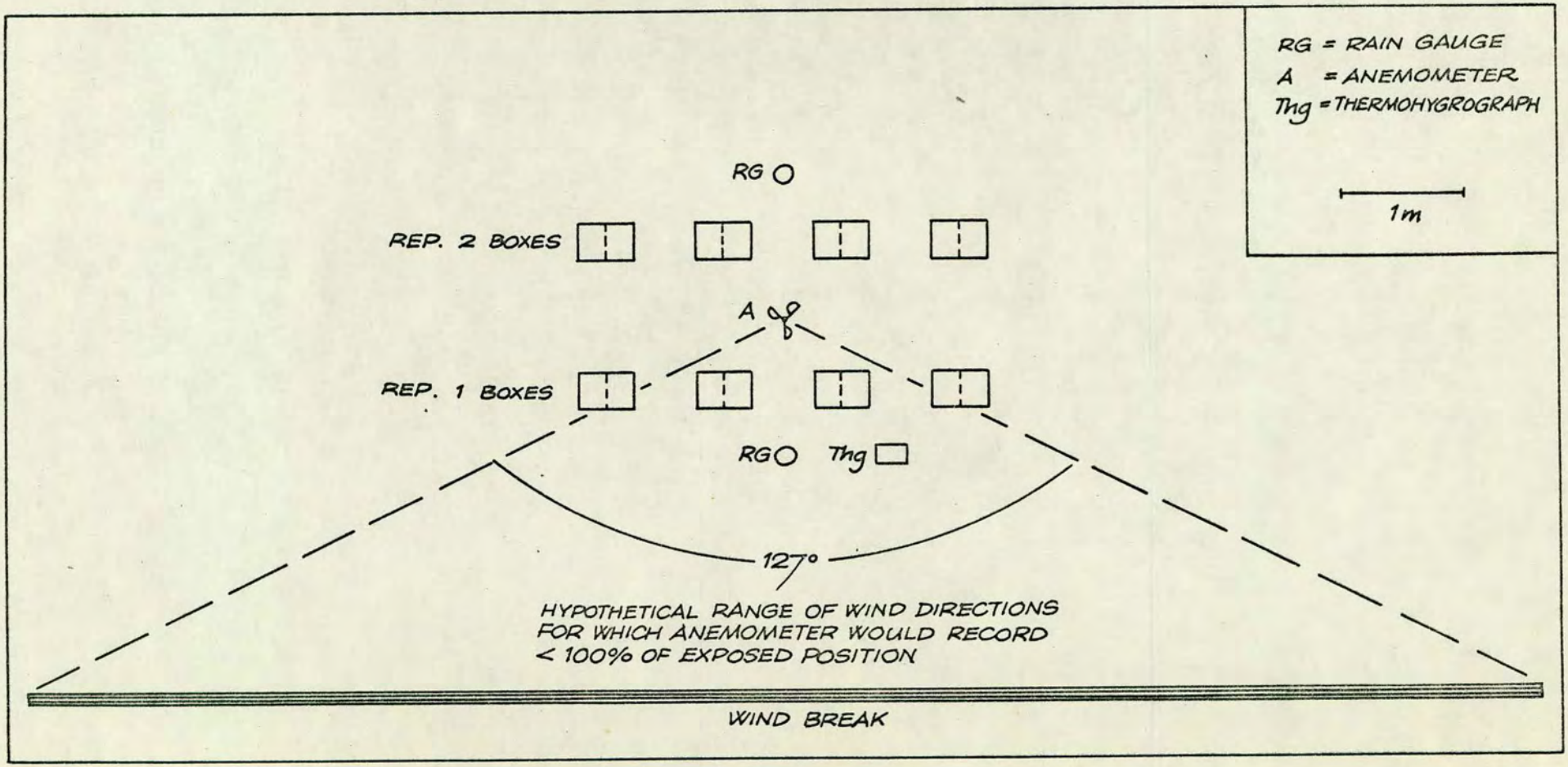


FIGURE 3,2 LIBERTON FIELD EXPERIMENT

LAYOUT OF A TYPICAL SHELTERED POSITION



by the provision of windbreaks. Because the logistics involved in sophisticated biological measurements would have been both inappropriate due to the experimental design and unacceptable because of the labour entailed, a balanced programme involving the use of relatively unsophisticated micrometeorological measurements was devised. This consisted of measurements of run of wind, rainfall, air temperature, relative humidity and soil temperature recorded at each position. In order to maintain a balance with the weekly intervals between tiller counts, the micrometeorological data was either recorded on or reduced to the same basis.

For measurements of run of wind, one Meteorological Office Mark 2B cup contact anemometer (Negretti and Zambra Ltd.) was used at each position. Before use the anemometers were calibrated over a range of windspeeds in the controlled environment wind tunnel. At each position the anemometer was placed central to the grass boxes as shown in Figure 3.2 and, except at the exposed position, at a distance of 2.5h from the windbreak. A lead was taken from each anemometer to a recording unit comprising 5 counters which was designed by Dr. R. Scott and constructed by Mr. J. Dyer. This unit, together with its source of power, two 12v car batteries, was housed in a larger box which was concealed to deter vandals. Inspections were carried out daily when possible but certainly at no greater time interval than 3 days.

Two standard 5" Meteorological Office rain gauges (Casella Ltd.) were installed at each position and were placed approximately 1.75h and 3.25h from the windbreaks as shown in Figure 3.2. Due to thefts, these were later replaced by non-standard gauges of a similar size.

Continuous records of air temperature and humidity were obtained

by means of thermohygrographs (Casella Ltd.). Before use, each instrument was calibrated individually in the laboratory. All 5 instruments were then simultaneously checked in the field by means of an Assman aspirated hygrometer (Casella Ltd.) before placing in position.

Soil temperatures were measured by means of thermistor probes (Grant Instruments (Developments) Ltd.) inserted into certain boxes. Instead of continuous monitoring from a central position, which would have created many problems with, for example, excessive lengths of wire, each probe was read on the recorder on one occasion each week, the day when tillers were counted. Thus, rather than use the automatic recording facility of this instrument, the probes were left to function as simple thermometers.

3.4 Experimental details

In this experiment, seeds were sown in shallow trays on 18.12.1969 and the seedlings transplanted into boxes on 7.1.1970. Any individuals not surviving were replaced on 22.1.1970 and 28.1.1970 after which date it was concluded that, because of competition, the successful growth of a transplant was unlikely. In any case, the success rate in transplanting was extremely high. The plants were then left to grow to a suitable size in the greenhouse. During this period soil temperature probes were inserted into the boxes in the 7.5 cm gap separating the 2 blocks of plants. In this way there was minimal disturbance of the plants themselves.

On 20.2.1970 the boxes were transferred to adjacent cold frames to harden off the plants which by that time had reached a suitable size. A heater installed in the frames helped to ward off any damage

which might have resulted from the severe frosts occurring at the time.

To provide a base line for future reference, a full count of all tillers was started on 2.3.1970 and completed on 6.3.1970. On 4.3.1970 the plants were clipped to a height of 8 cm to simulate a light grazing and the boxes placed outside for hardening off. On 6.3.1970 the fertilizer treatments were assigned and 25 g of urea or superphosphate were added as appropriate and then watered in. On 9.3.1970 the boxes were placed in a group on the hillside for further hardening off and then left for one week before moving to their assigned positions on 17.3.1970. This date was taken as the start of the experiment. The first tiller count took place on 24.3.1970 and then at weekly intervals until the final harvest. On 21.4.1970 many S.24 plants were found to have more than 20 tillers and one plant had 44. Further counting in S.24 was then abandoned until the final harvest. At that time S.170 had a maximum of 14 tillers and most plants had fewer than 10 thus causing no problems in counting.

Another reason for stopping counting was grazing damage by rabbits or hares. This was first noticed on 7.4.1970 during a routine tiller count. It was noticeable that S.24 suffered considerably more damage than S.170 perhaps reflecting its greater palatability. Also, those plants on the east facing side suffered most. It seems that not only did their grazing activities seriously detract from the value of this experiment but, whilst the damage was being inflicted, the rabbits, replete with S.24, were also able to enjoy the benefits of shelter from the predominantly westerly winds.

Control of grazing damage is a difficult problem especially in shelter experiments and has few solutions. The provision of cages necessarily alters the microclimate and in experimental situations

where microclimate differences are crucial, any interference is undesirable. Fencing the whole experimental area is impracticable if sufficient distance is to be kept between the fence and the experimental plants assuming that the effects of shelter may last up to a distance of 20h. By consulting with local farmers, it was discovered that Renardine is extensively used on farms as a rabbit repellant. By surrounding the experimental boxes with string soaked in this substance, any further grazing damage was prevented without, at the same time, affecting the microclimate.

S.170 was little affected by grazing damage and, since the tillers were also far easier to count, this species became the main interest of the experiment.

Throughout the experimental period no additional water was added in the field, however, a drought occurred towards the end of the experiment and at the first sign of prolonged wilting the experiment was terminated. The final destructive harvest started on 20.5.1970 and lasted one week.

3.5 Results of microclimatological measurements

With the measurements of run of wind, some initial difficulties were experienced with sources of power for the counter system and this unfortunately lead to the loss of data for the first 2 weeks. Thereafter, considerable vigilance was still required to ensure accurate readings. For instance, the 4-figure counter system was such that during periods of high winds, a complete cycle could take place in 1 or 2 days thus requiring frequent inspection. Also, the long shaft supporting the cups made precise vertical alignment critical and, unless this was frequently checked, vibrations developed when the anemometers were in motion. A further difficulty with this type of

anemometer was the hemispherical rather than conical cups. This further increased the tendency of such massive anemometers to over-estimate the run of wind because of the large angular momentum developed.

To convert from the number of counts to run of wind values in km, the individual calibrations were transformed to regression equations. These are shown in Table 3.1. The conversion was then carried out by substituting the number of counts in the appropriate equation. These equations illustrate the variation between the anemometers and it was therefore considered necessary to devise a means of checking their reliability. For this purpose it was assumed that there was minimal spatial variation across the site before the windbreaks were installed, that the windbreak was of negligible permeability and that windward shelter effects could be neglected. Alternatively, the latter two factors could be regarded as cancelling each other out.

With an infinitely long windbreak and with equal run of wind from all directions, the degree of shelter of each anemometer compared to an exposed control should be 50%. In fact the windbreaks were only 12.2 m long so that with the anemometers placed 3.05 m distant, the degree of shelter should be reduced to 35.2%. Therefore, after correction for calibration, the sum of the run of wind values at all the sheltered positions should be related to the run of wind value for the exposed position by the equation north + south + east + west = 2.59 x exposed. These values are shown in Table 3.2. A regression analysis showed the correlation coefficient between the two variables to be 0.985, a somewhat remarkable agreement. The values of run of wind were then converted to average windspeeds and these are shown for each position in Table 3.3.

LIBERTON FIELD EXPERIMENT

Table 3.1 Anemometer calibrations expressed as linear regressions.

Anemometer Position	Regression Equation
Exposed	$Y = -15.25 + 6.66\ (\pm 0.06)\ X$
North	$Y = -0.49 + 13.30\ (\pm 1.22)\ X$
South	$Y = 33.41 + 12.43\ (\pm 0.34)\ X$
East	$Y = -16.73 + 12.90\ (\pm 0.25)\ X$
West	$Y = -33.51 + 13.61\ (\pm 0.19)\ X$

X represents number of counts

Y represents run of wind in km

Table 3.2 Weekly run of wind from exposed and combined sheltered positions (km).

Days from start of experiment	Exposed value x 2.59	North + South + East + West
14 - 21	4234	4346
21 - 28	3010	2946
28 - 35	1703	1879
35 - 42	4951	4687
42 - 49	4177	4460
49 - 56	4110	4436
56 - 63	2153	2164

LIBERTON FIELD EXPERIMENT

Table 3.3 Mean weekly wind speeds ($m\ s^{-1}$).

Days from start of experiment	POSITION Exposed	North	South	East	West
14 - 21	2.70	1.83	1.73	2.18	1.44
21 - 28	1.92	0.82	1.10	1.61	1.34
28 - 35	1.09	0.29	1.07	0.73	1.02
35 - 42	3.16	1.77	1.56	1.63	2.79
42 - 49	2.66	0.79	2.38	1.77	2.43
49 - 56	2.62	1.49	2.23	2.45	1.17
56 - 63	1.37	0.65	1.22	0.85	0.87
MEAN	2.22	1.09	1.61	1.60	1.58

Table 3.4 Reduction in run of wind due to shelter (%).

Days from start of experiment	POSITION Exposed	North	South	East	West
14 - 21	0.0	32.1	36.1	19.3	46.5
21 - 28	0.0	57.1	42.8	16.1	30.3
28 - 35	0.0	72.9	1.6	33.2	6.2
35 - 42	0.0	43.8	50.7	48.3	11.8
42 - 49	0.0	70.2	10.6	33.6	8.7
49 - 56	0.0	43.2	14.9	6.7	55.4
56 - 63	0.0	52.9	11.4	38.1	37.0
MEAN	0.0	53.2	24.0	27.9	28.0

This table shows that throughout the experiment the exposed position experienced the highest mean weekly windspeeds. In the period 35-42 days from the start of the experiment, the winds were especially strong and in the exposed position amounted to 3.16m s^{-1}. The mean values for the experimental period as a whole show that the effect of shelter was greatest at the north position and very closely similar in the others although less pronounced.

If the efficiency of shelter produced is considered (cf. Caborn, 1971), it can be seen in Table 3.4 that the reductions in run of wind values, especially in the north position, were quite high and during one week amounted to 72.9%. By contrast, in the south position for the same week the reduction was only 1.6%.

These results, apart from their interest for this experiment, were a useful source of information in deciding the windspeeds in the wind tunnel yield experiments.

The measurements of air temperature were obtained from thermo-hygrographs which recorded continuously at each position. On being re-set the temperature readings were checked against the dry bulb reading on an Assman aspirated hygrometer (Casella Ltd.). These instruments were not always reliable and occasionally showed calibration shifts. Therefore the average maximum, minimum and mean values for all positions have been combined at weekly measuring intervals and these are shown in Table 3.5.

Another aspect of interest was the variation in temperature amplitudes. These are shown for each position in Table 3.6. The south position had the largest amplitude and the north the smallest. This difference may have been due to reflection from the shelter material by day and the greater accumulation of cold air by night, at the south

LIBERTON FIELD EXPERIMENT

Table 3.5 Mean daily maximum, minimum and mean air temperatures for each week (^{o}C) - all positions combined.

Days from start of experiment	Maximum	Minimum	Mean
0 - 7	12.2	- 0.2	6.0
7 - 14	10.9	1.8	6.4
14 - 21	8.6	- 0.2	4.2
21 - 28	9.3	- 0.9	4.2
28 - 35	15.8	5.3	10.6
35 - 42	15.2	2.9	9.1
42 - 49	13.6	2.3	8.0
49 - 56	7.9	2.5	5.2
56 - 63	11.9	3.0	7.5

Table 3.6 Mean daily air temperature amplitude at each position - all weeks combined (^{o}C).

POSITION				
Exposed	North	South	East	West
9.6	9.2	11.2	9.4	9.9

position. The experimental site, whilst free from minor topographic variations, sloped slightly downwards towards the north. Geiger (1961) described a situation in which barriers or shelterbelts acted as a dam to the downward passage of cold air on relatively calm nights and so it would appear that the east-west orientated windbreak in this experiment acted in a similar manner.

As explained previously, soil temperatures were only measured on the same day that tillers were counted i.e. at weekly intervals. These values were averaged over the whole experimental period for each position and the results are shown in Table 3.7. The temperatures were recorded in the afternoons which may partly explain why the boxes in the south position had the highest temperatures. Alternatively this could be a reflection of the greater amplitude in air temperatures. The reason why the west position, rather than the north position, had the lowest temperatures is not clear but it must be emphasised that the differences were very small.

The recording of relative humidity was abandoned shortly after the start of the experiment due to difficulties experienced in maintaining the calibration of the thermohygrographs in field conditions.

The measurement of rainfall was marred by the theft of the copper rain gauges. Where complete, the values for each week were averaged for the whole experimental period and the results are shown in Table 3.8. Rainfall at all positions was rather similar but the somewhat higher value of the exposed position would suggest some interception by the windbreak material or, alternatively, deflection during strong winds.

The micrometeorological data, although in some cases incomplete, showed that, as a result of the windbreaks, there were considerable differences in the various positions especially with respect to windspeed and, to a lesser extent, temperature.

LIBERTON FIELD EXPERIMENT

Table 3.7 Mean soil temperature at each position - all weeks combined (^{o}C).

POSITION				
Exposed	North	South	East	West
11.4	11.5	11.9	11.4	11.1

Table 3.8 Mean weekly rainfall at each position - all weeks combined (mm).

POSITION				
Exposed	North	South	East	West
7.1	6.9	6.9	6.8	6.9

3.6 Results of tiller counts

Of the various parameters assessed, the tiller counts provided the only means of monitoring growth on a weekly basis. Detailed examination of the increase in tiller number in relation to position and applied nutrients unfortunately revealed a somewhat confused picture. This was partly due to the technique by which 5 plants out of the central 8 in each block were selected at random each week for counting. With such limited replication it was particularly necessary to minimise experimental error and so, in retrospect, it would have been better to have counted the same plants on each occasion. Another difficulty in interpreting such readings is the typically exponential growth of young plants, thus making the final tiller number critically dependent on the initial tiller number. This aspect was taken into account by comparing the number of tillers of all plants each week with the original number counted just before the start of the experiment. The number of tillers on a particular occasion was then expressed as a percentage of the original. The results are shown in Figure 3.3 for S.24 and Figure 3.4 for S.170, with all levels of nutrients combined for each position.

With S.24, the final tiller numbers expressed as percentages were largest in the south position followed by the exposed, east, north and west positions. This picture has probably been distorted by missing values and because of the gap in the tiller counts, is of doubtful reliability.

With S.170, a clearer and rather different picture emerged; the largest increases occurred in the east and west positions followed by the south, north and exposed positions. In S.170, for the P_2 N_2 treatment alone, there was a similar result but with a reversal of the relative positions of the north facing and exposed plots. This is

FIGURE 3.3 LIBERTON FIELD EXPERIMENT
S.24 NUMBER OF TILLERS PER PLANT EXPRESSED AS % OF ORIGINAL
ALL NUTRIENTS COMBINED

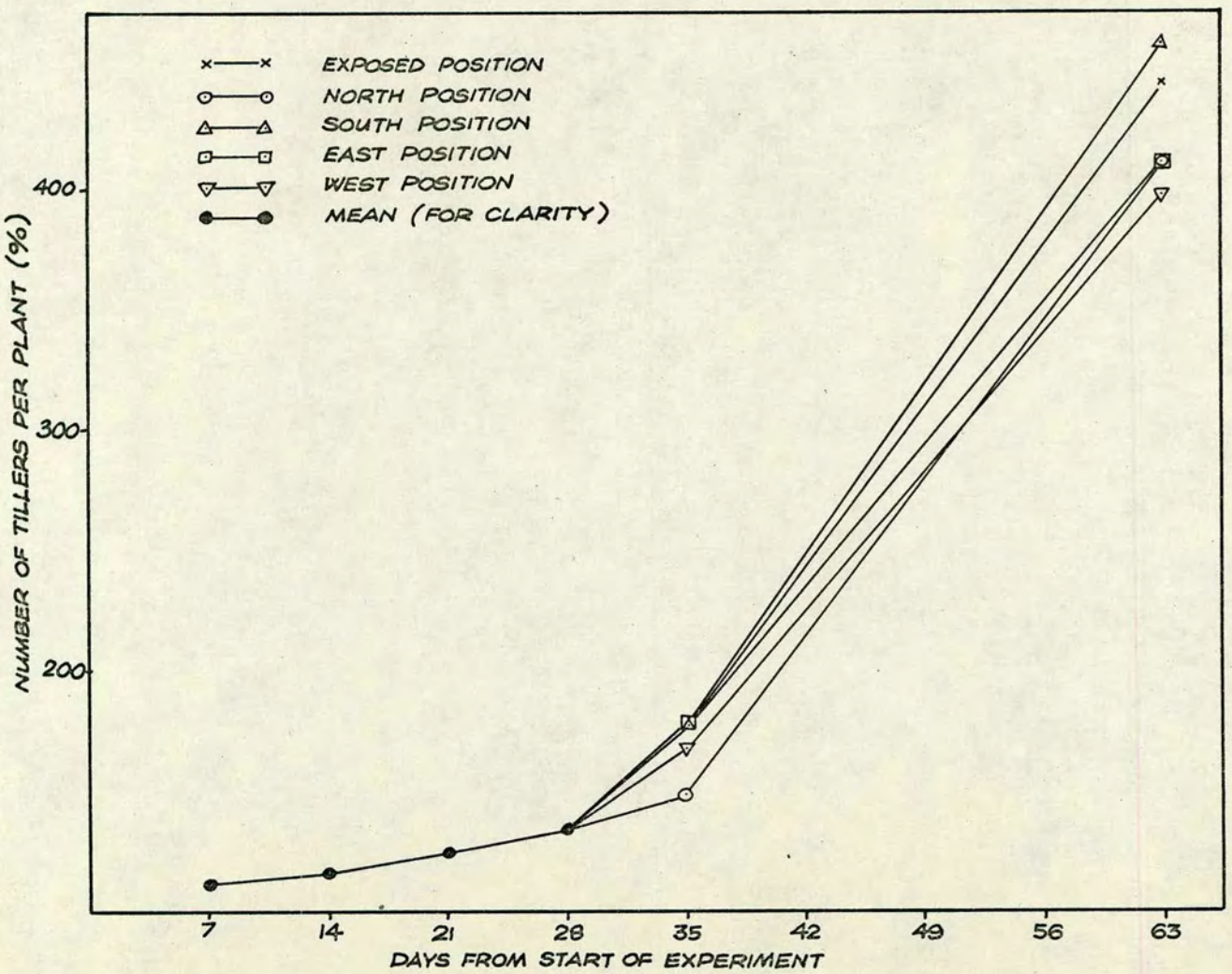


FIGURE 3,4 LIBERTON FIELD EXPERIMENT

S.170 NUMBER OF TILLERS PER PLANT EXPRESSED AS % OF ORIGINAL
ALL NUTRIENTS COMBINED

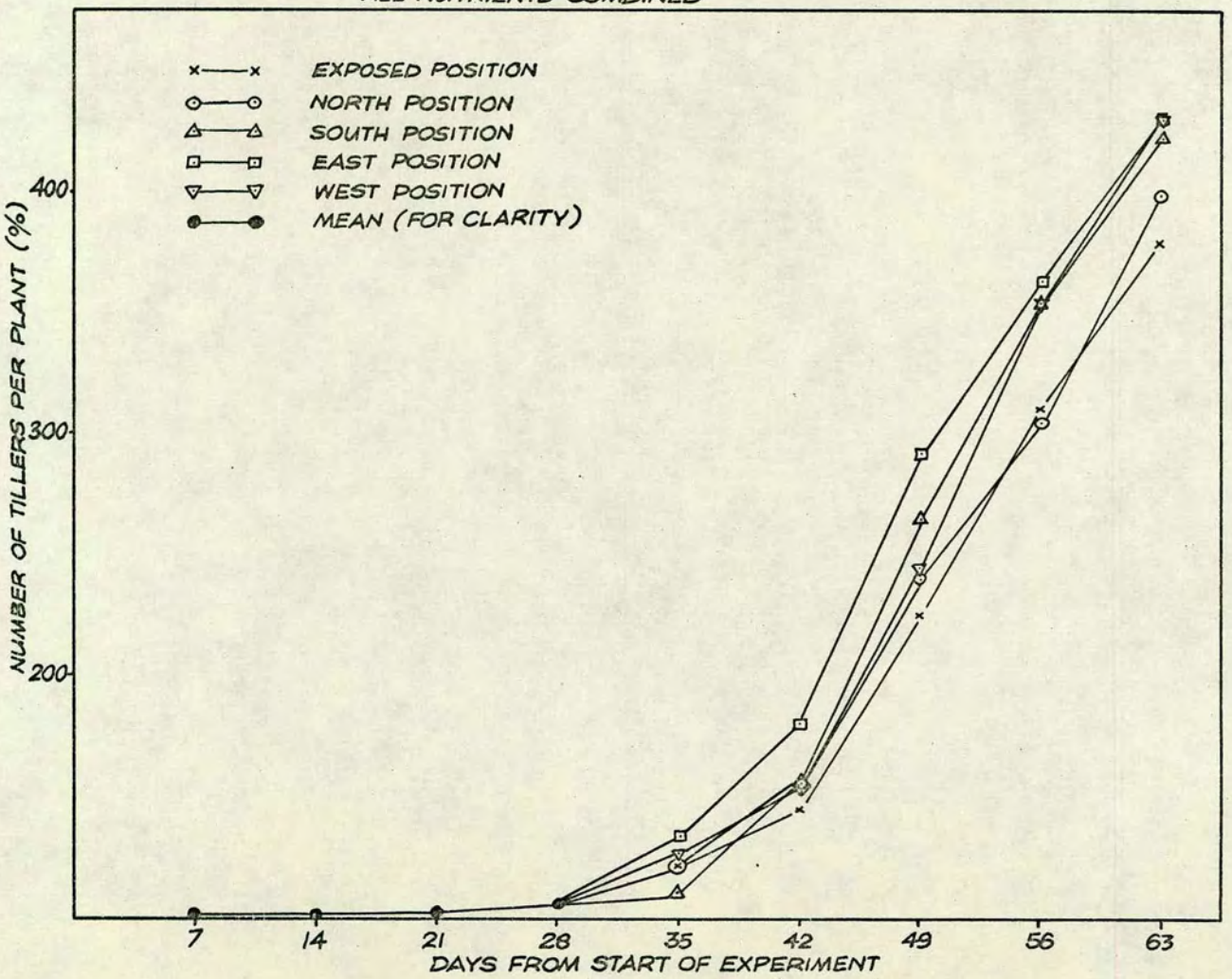
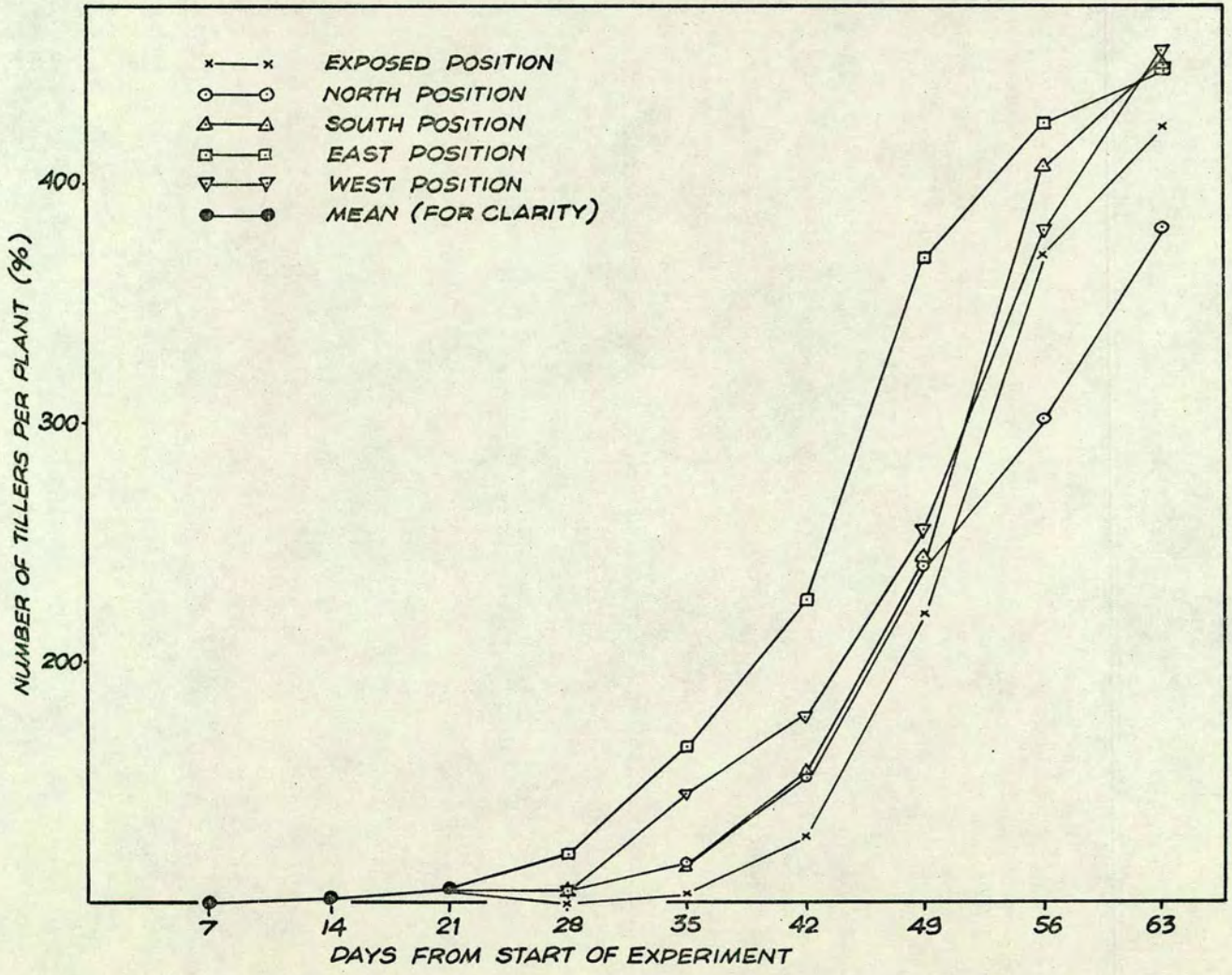


FIGURE 3.5 LIBERTON FIELD EXPERIMENT
S 170 NUMBER OF TILLERS PER PLANT EXPRESSED AS % OF ORIGINAL
P_2N_2 TREATMENT



shown in Figure 3.5.

If the initial number of tillers is multiplied by the percentage increase each week, a new hypothetical tiller number can be produced. This value was used to calculate the relative rates of increase of tillers over the whole experimental period using a formula analogous to the relative growth rate concept normally applied to the differences between dry weights. Table 3.9 shows these values expressed as the mean number of tillers produced per tiller per week for S.170. The exposed position had the lowest value, again suggesting a beneficial effect of shelter, but the highest value at the west position is difficult to explain.

This was not reflected by the final numbers of tillers per plant at the west position, expressed as the mean of all nutrient levels, as is clear from Table 3.10. This shows the final number of tillers of S.170 at all positions and for all nutrient levels. The east position had the highest mean value but the west position had the highest individual value in the P_2N_2 treatment. Both the exposed and north positions had generally lower values than the rest. However, this data was not conclusive as an analysis of variance showed that only the differences between nutrients were significant and then only at the 5% level.

3.7 Results of dry weights

The analysis of dry weights was marred by the loss of plots due to rabbit damage but nevertheless produced some useful information. The mean values for the two replicates are shown in Table 3.11 for S.24 and Table 3.12 for S.170.

In both species, the yield of the east position was the highest

LIBERTON FIELD EXPERIMENT

Table 3.9 S.170 Mean relative rates of tiller increase (tillers $tiller^{-1}$ wk^{-1}).

POSITION				
Exposed	North	South	East	West
0.148	0.156	0.156	0.161	0.176

Table 3.10 S.170 Final harvest - mean number of tillers per plant.

Nutrient treatment	POSITION					
	Exposed	North	South	East	West	Mean
P_1N_1	17.06	16.61	18.45	20.74	19.01	18.37
P_1N_2	16.33	20.30	21.40	21.77	18.68	19.70
P_2N_1	18.94	16.39	18.64	20.94	18.86	18.75
P_2N_2	18.82	17.19	21.71	22.96	26.45	21.43
MEAN	17.79	17.62	20.05	21.60	20.75	19.56

LIBERTON FIELD EXPERIMENT

Table 3.11 S.24 - Final harvest
- mean dry weight per plant (mg).

Nutrient treatment	POSITION Exposed	North	South	East	West	Mean
P_1N_1	1314	1046	1416	1093[1]	1438	1261
P_1N_2	1794	1344	1452	1909	1581	1616
P_2N_1	1353	1280	696[2]	-	1278	-
P_2N_2	1574	1581	1956	1697	1686	1699
MEAN	1509	1313	-	-	1496	-

1. One replicate only
2. One replicate only with some rabbit damage

Table 3.12 S.170 Final harvest
- mean dry weight per plant (mg).

Nutrient treatment	POSITION Exposed	North	South	East	West	Mean
P_1N_1	819	648	818	924	623	766
P_1N_2	556	790	818	821	772	751
P_2N_1	748	716	690	925	839	784
P_2N_2	765	700	823	1057	1021	873
MEAN	722	714	787	932	814	

but the relative yields in the other positions varied. The sequence in decreasing order of yield in S.24 was east, exposed, west, south and north and in S.170, east, west, south, exposed and north. Each box was planted with two monoculture blocks of grass, so that if the responses of the two species to the imposed environments were similar, one would expect their dry weights to be correlated. If they were highly correlated, it might even have been possible to derive values for the S.24 plots damaged by rabbits. A regression analysis of the yield of S.24 against the yield of S.170 produced the equation:

$$Y = 10.099 + 0.274\ (\pm\ 0.316)\ x$$

However, the correlation coefficient was only 0.147 and this possibility was therefore discounted.

The dry weights were further examined by analysis of variance. Plants of S.24 in the exposed and west positions were not damaged by grazing and so, instead of analysing the whole experiment, a split, split plot design rendered highly unwieldy by the missing plots, these two positions were analysed with S.24 and S.170 together. The differences between the two species in both cases were significant at the 0.1% level but of more interest was the difference between the first order species x position interactions. These were significant at the 10% level in the exposed position but not significant in the west position. Whilst 10% significance would not normally be acceptable, it does suggest that under more exposed conditions, the response of S.170 to nitrogen was reduced compared to that of S.24. The data for S.170 were complete throughout and so allowed for a standard analysis of variance. The results of this analysis showed that neither nutrients, position or the interactions were significantly different.

LIBERTON FIELD EXPERIMENT

Table 3.13 S.170 Nitrogen and Phosphorus contents of shoots (%).

	Treatment			
	P_1N_1	P_1N_2	P_2N_1	P_2N_2
Nitrogen	1.97	4.42	2.28	4.43
Phosphorus	0.41	0.52	0.55	0.61

One possible explanation for this result is that the nutrient levels applied were not sufficiently different to be sensibly regarded as separate treatments. The nitrogen and phosphorus contents of S.170 (expressed as means for all positions) are shown in Table 3.13. An analysis of variance on the nitrogen contents of S.170 showed that the differences between the high and low levels of nitrogen were significant at the 0.1% level and that the first order nitrogen x position interaction was significant at the 10% level. Thus, the differences in nitrogen levels applied were certainly large enough to constitute discrete treatments but this was not reflected in the final yields. The first order interaction would suggest that the ability of S.170 to take up nitrogen may be determined by the degree of shelter.

The final harvest in S.170 was carried out to allow the effects of shelter on the constituents of yield to be determined. However, in view of the inconclusive nature of the yield results as a whole, more detailed analysis was considered inappropriate.

3.8 Conclusions

These results would seem to be more appropriate for inferences rather than definite conclusions. It is clear that there was a definite reduction in windspeed due to shelter but it would have been very useful to have had similar information about the effects on air temperature. It would therefore seem reasonable to regard the reduction in windspeed at least as a contributory factor in the yield differences obtained. These results are considered further in Chapter 5.

CHAPTER 4.

LAMMERMUIRS FIELD EXPERIMENT

4.1 Introduction

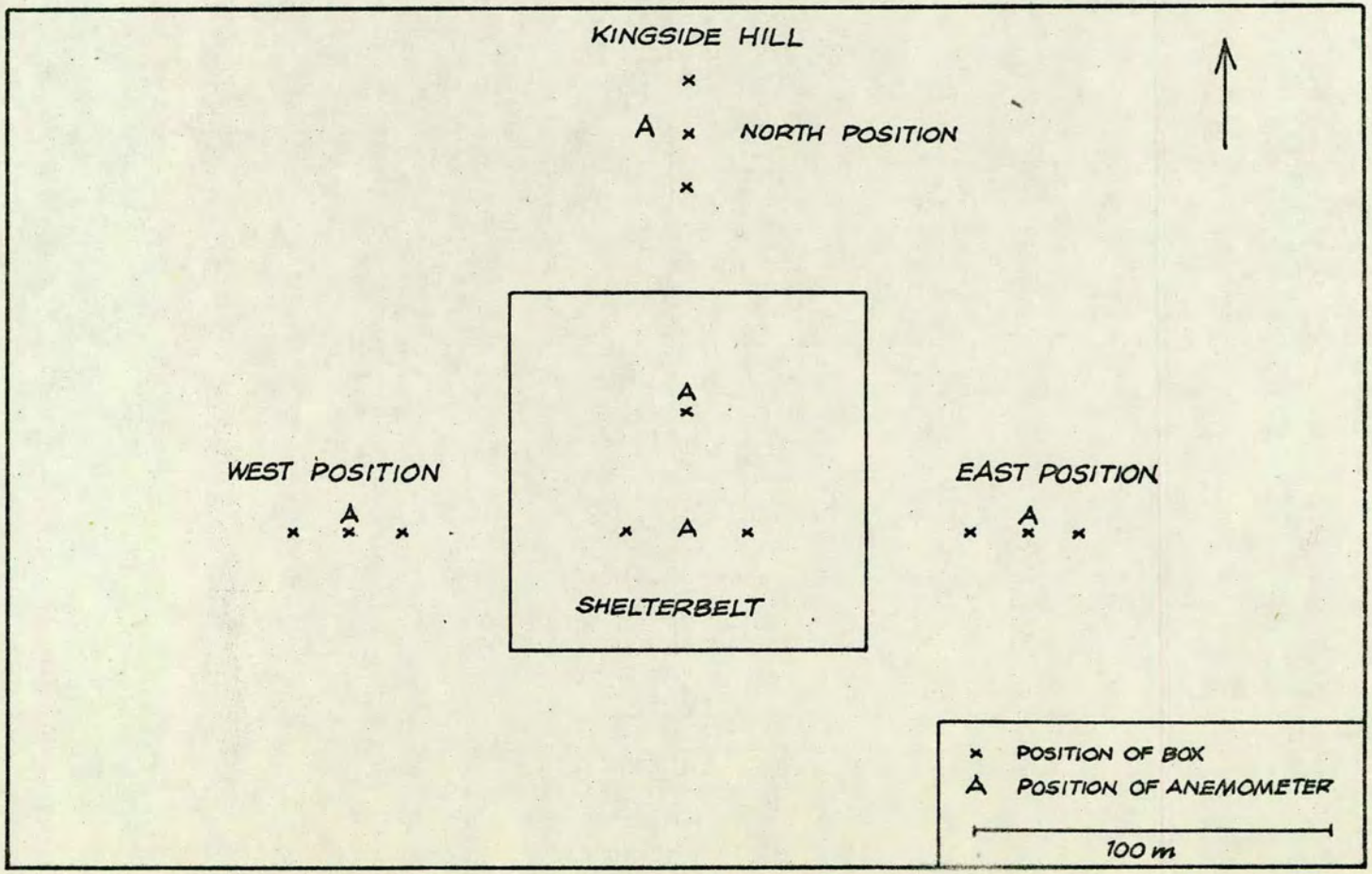
The object of this experiment was to investigate whether the shelter produced by a natural shelterbelt could affect the growth of grass in spring. Intended to be far less elaborate than the previous experiment, the effects of different nutrient regimes were excluded. In designing this experiment the following questions were considered :

1. How does shelter from a natural shelterbelt affect the early spring growth of S.24 Lolium perenne and S.170 Festuca arundinacea ?
2. How is this influenced by the direction of shelter ?
3. What are the microclimatological differences produced by shelter and to what extent can they be related to differences in plant growth ?

4.2 Experimental design

In this experiment only 12 boxes were used and they were placed in positions exposed to winds from the east, west and north and actually within the shelterbelt. Outside the shelterbelt, single boxes were placed 2h, 3h and 4h distant in 3 directions and regarded as replicates. To incorporate the comparison of the 2 species, each box was again planted in the form of 2 monoculture blocks. The general experimental layout is shown in Figure 4.1.

FIGURE 4.1 LAMMERMUIRS FIELD EXPERIMENT GRID REFERENCE NT 634647
LAYOUT OF EXPERIMENTAL SITE



4.3 Microclimatological measurements

Reflecting the less elaborate biological nature of this experiment, the instrumentation was also reduced. The main emphasis was on run of wind measurements but the programme also included rainfall, air temperature and soil temperature.

For measurements of run of wind, the Meteorological Office supplied 5 Mark 2b cup counter anemometers. Reading in units of .01 miles, these anemometers provided convenient and reliable information at the weekly intervals required. Before placing in the field they were calibrated in the controlled environment wind tunnel. In contrast to the anemometers used at Liberton, these instruments were found to agree closely with each other. During the experiment 1 anemometer developed a fault and was subsequently replaced. Of the 5 anemometers used, 3 were placed outside the shelterbelt at the 2h positions occupied by the boxes and the remaining 2 were located within the shelterbelt. To obviate the effects of the more pronounced topographic variation to be found at this site, each anemometer was mounted on a tripod 1m above the ground.

For rainfall measurements one rain gauge was located close to each of the 12 boxes. This number was later reduced to 7 on 22.4.1970 to make up for those stolen at the Liberton site.

Air temperature was monitored continuously by 1 thermograph (Cassella Ltd.) until 15.4.1970 and, after this date, a further 3 instruments were added to allow for detailed measurements at each position until the end of the experiment. Measurements of soil temperature were taken with 2.5 cm soil thermometers placed in the boxes. These were read each time the site was visited i.e. at weekly intervals. The same criticism of the relevance of such spot tempera-

ture measurements to the temperature experienced by the plants over a whole week applies here as in the case of the thermistor temperature probes at Liberton.

4.4 Experimental details

The experimental approach closely followed that of the Liberton experiment. The boxes were planted with seedlings on 8.1.1970 and then treated as before until 11.3.1970 when the boxes were taken out to the site. In contrast to the Liberton experiment, no nutrients other than those required for the basic U.C. mix were added. The boxes were placed in their assigned positions on 18.3.1970 when the experiment started. Because of the presence of sheep, Highland cattle and some rabbits near the site, each box was enclosed in a specially constructed cage 1.52 m long by 0.91 m wide by 0.61 m high. Constructed of a light framework of 1 cm steel, these cages supported a 5 cm mesh covering of chicken wire which was intended to provide the maximum protection from grazing consistent with the minimum obstruction of airflow. This arrangement worked successfully until the penultimate week of the experiment when several boxes were grazed by young rabbits able to penetrate the mesh. This damage was again confined to S.24 and destroyed any meaningful yield data from 3 boxes.

The initial tiller count took place on 7.3.1970 and then at weekly intervals once the experiment had started. Again, the weekly counting of tillers in S.24 had to be abandoned towards the end of the experiment because of the density of the sward. Some boxes, especially at the east position, were observed to have wilting plants when counted on 6.5.1970, but this was corrected by later rainfall. The plants were removed from the field on 27.5.1970 and the final harvest

started on 1.6.1970 and completed on 3.6.1970. The procedure used was the same as in the Liberton experiment.

4.5 Results of microclimatological measurements

The readings in miles per week on the anemometers were converted to average windspeeds in ms^{-1} and these are shown in Table 4.1. The readings from the 2 anemometers within the shelterbelt have been averaged for this purpose and the final mean values derived from those weeks for which there was complete data. The north position had consistently the highest windspeeds, the other positions varying in relation to each other. For the experimental period as a whole, the lowest mean windspeed was recorded at the east position. Compared to the Liberton experiment, the mean windspeeds were generally higher. This was especially so during the last week of the experiment when the mean windspeed at the north position was 6.74 m s^{-1}. This difference may partly have been due to the more exposed aspect of the site and partly to the anemometers being positioned at a height of 1m.

The air temperature measurements, as in the Liberton experiment, were not regarded as being of sufficient reliability to evaluate the conditions at each position. For weeks when there was more than one thermograph available the values for all positions were averaged. These results are shown in Table 4.2. It can be seen that the early part of this experiment was carried out under quite severe conditions.

For measurements of soil temperature, the thermometers were distributed with 1 in the shelterbelt and 2 at each of the other 3 positions. The values were reduced to means for the whole experimental period for each position. These are shown in Table 4.3.

LAMMERMUIRS FIELD EXPERIMENT

Table 4.1 Mean weekly windspeeds ($m\ s^{-1}$).

Days from start of experiment	POSITION East	West	North	Shelterbelt
7 - 14	1.63	2.97	5.28	2.82
14 - 21	1.78	2.07	-	2.04
21 - 28	2.08	1.45	2.95	1.44
28 - 35	-	-	-	-
35 - 42	2.66	3.86	5.74	3.95
42 - 49	4.50	3.93	4.53	4.00
49 - 56	2.84	2.86	3.86	2.27
56 - 63	1.53	1.52	3.95	1.73
63 - 70	2.91	4.93	6.74	4.64
MEAN[1]	2.67	3.42	5.12	3.34

1. Mean of all complete weeks

Table 4.2 Mean daily maximum, minimum and mean air temperatures (^{o}C) - all positions combined.

Days from start of experiment	Maximum	Minimum	Mean
0 - 7[1]	8.2	- 0.7	3.8
7 - 14[1]	3.2	- 2.0	0.6
14 - 21[1]	4.9	- 1.9	1.5
21 - 28	4.9	- 1.4	1.8
28 - 35	10.7	3.2	7.0
35 - 42	10.1	1.4	5.8
42 - 49	15.8	6.5	11.2
49 - 56	10.0	3.9	7.0
56 - 63	15.1	6.3	10.7
63 - 70	15.3	6.2	10.8

1. One thermograph only

LAMMERMUIRS FIELD EXPERIMENT

Table 4.3 Mean soil temperature at each position (^{o}C).

POSITION			
East	West	North	Shelterbelt
9.2	8.3	8.5	6.1

Table 4.4 Mean weekly rainfall at each position (mm).

POSITION			
East	West	North	Shelterbelt
11.2	10.8	10.6	5.8

With the rainfall values, there were marked differences at each position and so these results were converted to means for each position over the whole experimental period. These are shown in Table 4.4. The particular point of note here was the low value within the shelterbelt itself which was probably a reflection of interception by the trees. Outside the shelterbelt the differences were relatively small and may have been reflections of local topographic variation.

4.6 Results of tiller counts

In the same way as in the Liberton experiment, the weekly increases in tiller number were converted to percentage values and these are shown in Figure 4.2 for S.24 and Figure 4.3 for S.170. The results for S.24 are of doubtful reliability but in S.170, the north position showed the greatest increase. There seemed to be no obvious reason for this. The smallest increase occurred within the shelterbelt, a predictable result in view of temperature and shading effects. These results were confirmed by the values for relative rates of tiller increase. (Table 4.5.).

The final tiller numbers per plant for both species are shown in Table 4.6. This parameter showed a different response when expressed in absolute terms rather than percentage terms. This was especially so for S.170 at the north position relative to the other positions. Although the data for S.24 were incomplete,it appeared that this species was far more responsive to the different environments than S.170. The highest numbers were recorded, the east position for S.24 and the west position for S.170. However, the analysis of variance of S.170 showed that the differences between the means were not significant.

FIGURE 4.2 LAMMERMUIRS FIELD EXPERIMENT
S 24 NUMBER OF TILLERS PER PLANT EXPRESSED AS % OF ORIGINAL
ALL NUTRIENTS COMBINED

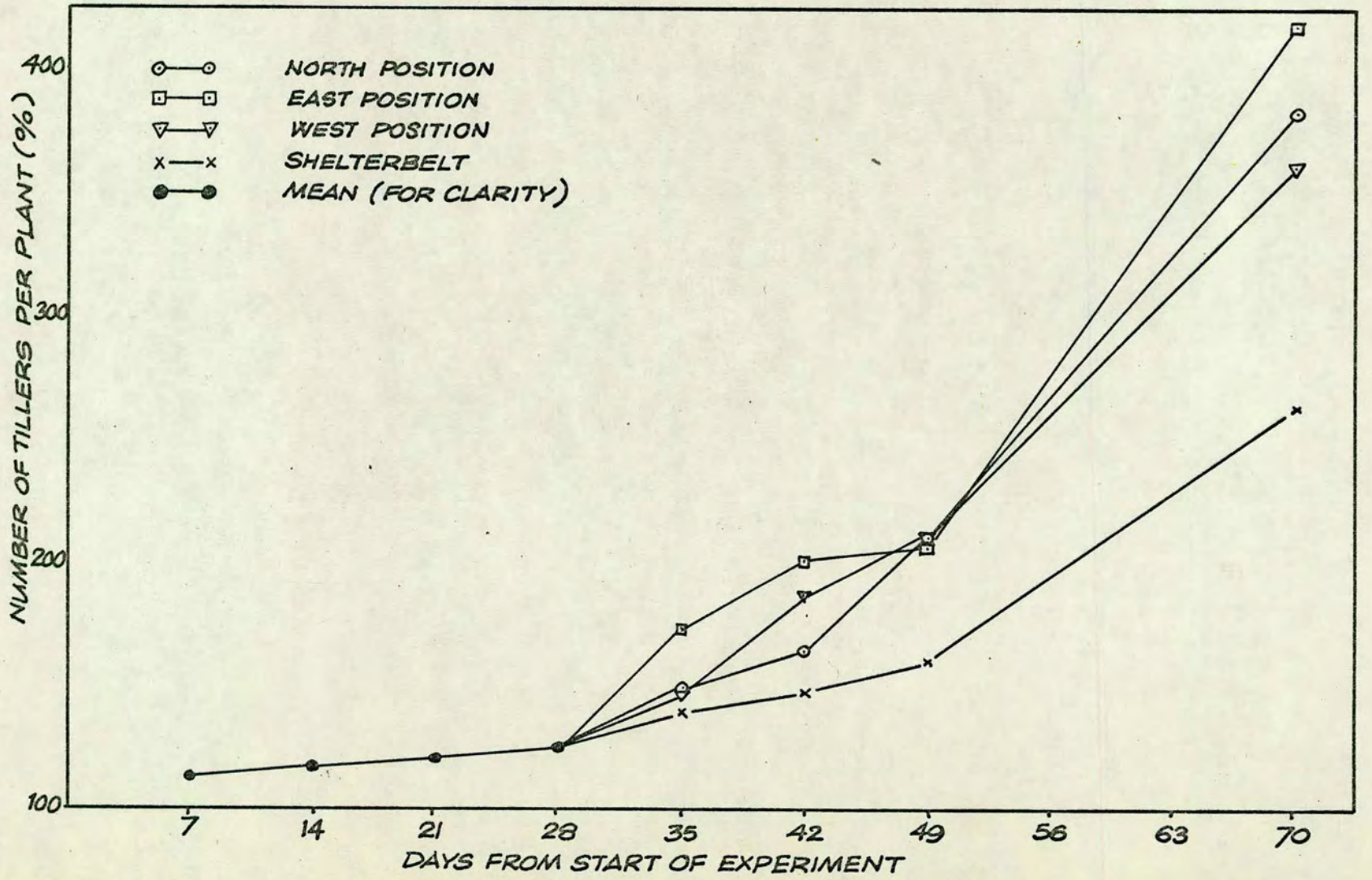
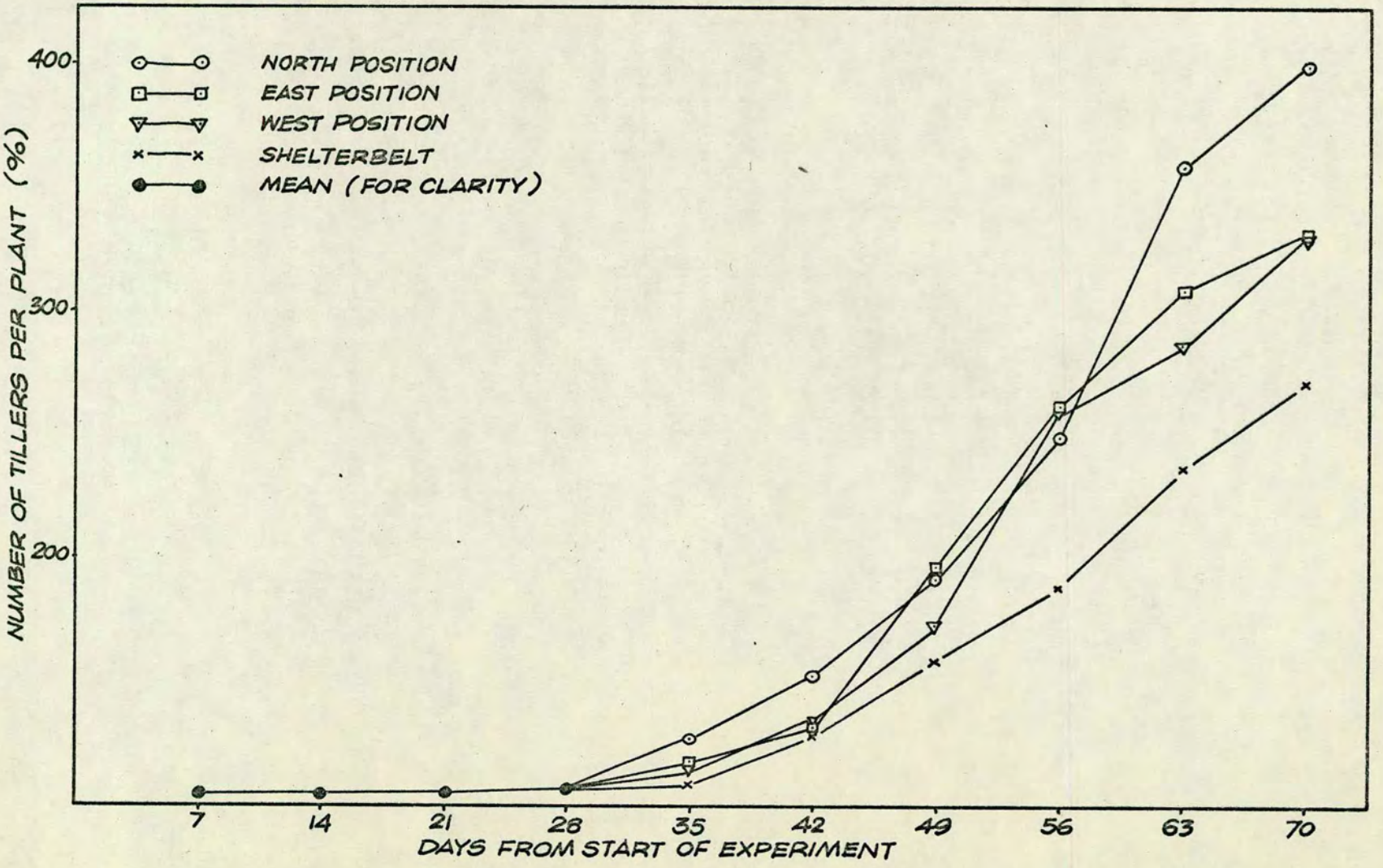


FIGURE 4,3 LAMMERMUIRS FIELD EXPERIMENT
S170 NUMBER OF TILLERS PER PLANT EXPRESSED AS % OF ORIGINAL
ALL NUTRIENTS COMBINED



LAMMERMUIRS FIELD EXPERIMENT

Table 4.5 Mean relative rates of tiller increase (tillers tiller^{-1} wk^{-1}).

Species	POSITION East	West	North	Shelterbelt
S.170	0.109	0.109	0.126	0.091

Table 4.6 Final harvest - mean number of tillers per plant.

Species	POSITION East	West	North	Shelterbelt
S.24	43.25	37.69[1]	36.75	26.75[1]
S.170	13.29	13.92	13.71	11.13

1. Values from 2 boxes only.

Table 4.7 Final Harvest - mean dry weight per plant.

Species	POSITION East	West	North	Shelterbelt
S.24	1213	1106[1]	1069	804[1]
S.170	618	570	550	472

1. Values from 2 boxes only.

4.7 Results of dry weights

The mean dry weights per plant of both species at the final harvest are shown in Table 4.7. In S.24 these reflected the numbers of tillers per plant but not in S.170. Both species responded similarly and yields were highest at the east position. An analysis of variance for the S.170 data again showed that the differences between the means were not significant. Part of the reason for this was the large F ratio for replicates which was actually significant at the 10% level. This would suggest that to regard the 3 boxes at each position as separate replicates rather than different treatments was probably not justified.

4.8 Conclusions

In view of the variability of these results it was considered that to draw any definite conclusions from this experiment concerning the effects of shelter would be unjustified. It could perhaps be inferred that shelter from westerly winds was of some advantage.

One reason why the responses were not clear could have been that the levels of nitrogen and phosphorus corresponded to the P_1 and N_1 levels at Liberton. In retrospect, this was perhaps unfortunate since the results from the Liberton experiment suggested that responses to shelter were more likely at higher levels of nutrients.

These results will be further considered in Chapter 5.

CHAPTER 5.

GENERAL DISCUSSION OF THE FIELD EXPERIMENTS

5.1 Introduction

These two experiments, involving considerable effort in execution, are disappointing in the amounts of concrete information that they produced. This was largely due to the minimal replication, a consequence of having taken the view that with the limited resources available, it was more appropriate to take a wide look at the situation in the field rather than to aim primarily for statistical significance from experiments with more limited objectives. In retrospect, it can be argued that the time and effort expended in these early experiments did not justify the quality of the results obtained. However, there has been no similar field work in eastern Scotland, and, had the alternative laboratory approach been adopted, its conclusions would have been of unknown relevance.

5.2 General weather conditions

In drawing general conclusions about these experiments, it is important to know how typical the conditions experienced during the experimental period were of those in spring in eastern Scotland. This can be ascertained by reference to the appropriate Monthly Weather Reports (Meteorological Office, 1970).

In March, it was generally windy with gales reported on 14 days in Scotland especially in the period from the 16th to the 18th. It was also cold with a mean air temperature of 1.3^{o}C below average. Rainfall was about 80% of average and the sunshine values above average.

In April it was less windy with gales on 8 days in Scotland.

Mean temperatures were also below average by 1.5°C and rainfall was 4% below average. Sunshine was 5% above average.

May was again less windy with gales on only 5 days. Mean temperatures were 0.8°C above average but sunshine was only 72% of average due to the frequent occurrence of sea fogs. Rainfall was only 61% of average and this probably accounts for the drought that occurred towards the end of both experiments.

Throughout the whole period, the below average rainfall was, perhaps, the most noticeable feature. In true field conditions this would have been a period in which any effects of shelter would have been expected to have been more pronounced (Marshall, 1967). Otherwise, the spring as a whole was not particularly unusual.

5.3 Conclusions

Despite the inconclusive nature of much of the data there were certain inferences that could usefully be drawn. These were:

1. The growth of S.24 Lolium perenne followed a different pattern from S.170 Festuca arundinacea.
2. S.170 was a much more convenient experimental material.
3. Both species seemed to show enhanced growth due to shelter but the response was less obvious in S.170 than in S.24.
4. Any responses to shelter were more pronounced at high levels of nitrogen and phosphorus or high levels of nitrogen alone.
5. In the Liberton experiment, shelter from the east or the west appeared to be the most effective; in the Lammermuirs

experiment there appeared to be some advantage in shelter from the west.

6. In the Liberton experiment there was a tendency for exposed plants to make up for their slower earlier growth during the last week of the experiment. This could have been due to the earlier attainment of an optimum leaf area index as suggested by Marshall (1974) or alternatively, a differential effect of drought.

7. The effect of the microclimatic changes produced by shelter were difficult to assess because of the variability of the biological data.

8. Shelter had a considerable effect in reducing wind and so this must be considered as a possible causal factor.

9. Whilst the microclimatological data were not always very reliable, a useful insight into conditions in spring in eastern Scotland was produced.

It was considered that the implications of these experiments warranted further exploration of the possible effects of wind on the growth of grass by the use of the controlled environment wind tunnel.

SECTION 3.

THE CONTROLLED ENVIRONMENT WIND TUNNEL

CHAPTER 6.

THE CONTROLLED ENVIRONMENT WIND TUNNEL

6.1 Introduction

Central to much of the experimental work in this thesis has been the use of the controlled environment wind tunnel. The design objectives of this low speed wind tunnel at the Department of Forestry and Natural Resources were to combine good aerodynamic properties with a standard of temperature and humidity control acceptable for experiments with plants or animals. These objectives have, on the whole, been successfully achieved by the use of a closed circuit or Prandtl tunnel incorporating a bypass system for air conditioning.

T.E.M. Engineering Limited were responsible for the supply and installation of the main body of the wind tunnel and subcontracted the air conditioning system to Jeffair Limited.

6.2 Design and construction

Figure 6.1 shows a plan of the wind tunnel using standard nomenclature (Pankhurst and Holder, 1965; Pope and Harper, 1966). Air flow is in a clockwise direction generated by the main axial fan located just after the second corner.

The main structural support for the wind tunnel is provided by steel frameworks diagonally mounted at each of the 4 corners. A wooden connecting framework supports the body of the wind tunnel which is lined internally with 0.6 cm marine plywood. Insulation is provided in all areas by 5 cm expanded polystyrene sheeting, exceptions being the circular fan section where felt is substituted and the working section which is a separate unit. Finished off internally to a high standard of workmanship to ensure restricted growth of the

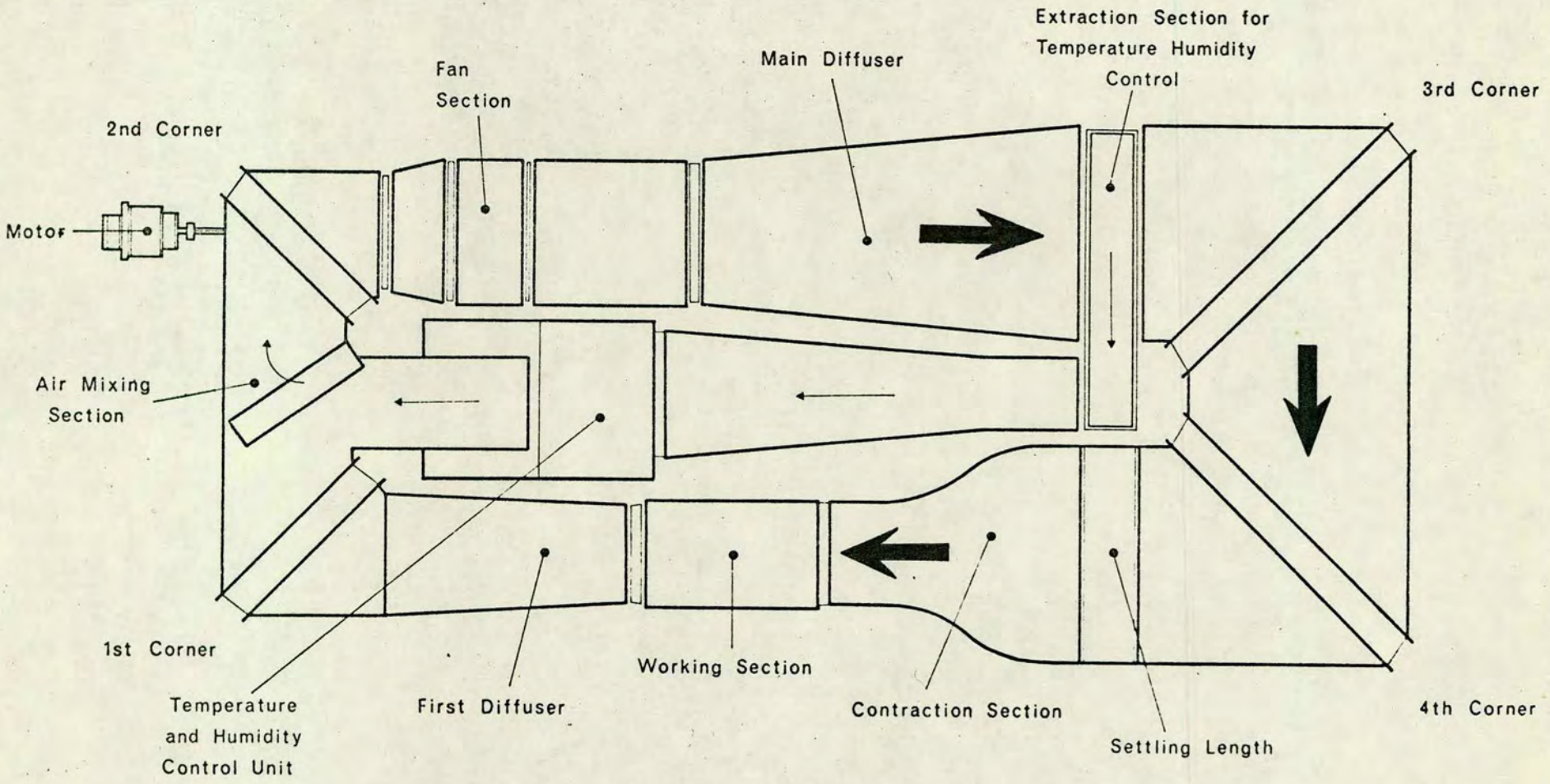


FIGURE 6,1

CONTROLLED ENVIRONMENT WIND TUNNEL

0 1 2 3 4 5
METRES

boundary layer, the walls are completed externally with a layer of 0.6 cm hardboard.

All corners in the wind tunnel are fitted with turning vanes supported by the steel frameworks. Corners 3 and 4 are identical whilst 1 and 2 have fewer vanes because of differences in the dimensions of the duct.

Immediately before the third corner, air is withdrawn through 8 circular holes into a channel approximately 4m in length leading to the air conditioning unit. The withdrawal of air at this point is apparently a practice of common occurrence (Gorlin and Slezinger, 1964). Air passing through this unit is expelled by the action of the centrifugal fan and then split into 2 channels before re-entering the main air stream prior to the second corner. Two adjustable vents can be used to regulate the flow of the conditioned air.

The overall dimensions of the wind tunnel are approximately 12m x 6m and the total volume of air enclosed is 566 m^3. Proceeding in a clockwise manner and starting at the leeward end of the working section, the dimensions at this point are 0.94m wide by 0.69m high. The first diffuser is 2.40m long and the use of an equivalent cone of 5^o total included angle increases the width to 1.15m at the first corner to guard against boundary layer separation (Bradshaw and Pankhurst, 1964). Vertically, there is a small expansion from 0.69 to 0.76m within the diffuser and then a sudden increase to 1.15m to incorporate the returning air from the air conditioning by-pass system after the first corner. These dimensions are maintained round the second corner, a further expansion occurring in the pre-fan transition section when the channel becomes circular with a diameter of 1.37m. The aft-fan transition section resumes the square

dimensions, again of 1.37m and this leads into the main diffuser. 3.66m long, this diffuser has an 11^{o} total included angle which increases the channel width to 2.06m. Vertically there is a slight expansion to 1.53m. At this point the tunnel has its maximum dimensions which are retained past the third and fourth corners until the contraction section is reached. This section has a 5:1 contraction ratio and reduces the air flow to the working section dimensions of 0.92m wide x 0.69m high into which it leads.

The working section is completely removable to allow the wind tunnel to be used for a variety of purposes. As designed for experimental work on plants, it consists of a chamber lined with 3 layers of 0.6 cm plate glass to allow for visibility and good insulation. The chamber is 1.83m in length and gradually widens by 0.02m to 0.94m, the width of the first diffuser. This minimizes the growth of the boundary layer on the side walls but the height remains constant. The floor is in the form of a box, 0.25m deep into which container-grown plants can be placed with soil levels flush with the floor of the wind tunnel. Electro-mechanical lifting gear for raising and lowering the working section floor to handle experimental material is incorporated into the system. Micro-switches restrict the range of vertical travel whilst a hand-operated winding gear permits fine adjustment of the floor level and effective sealing.

6.3 Aerodynamic design considerations

Aerodynamically, this wind tunnel was designed to produce an air flow which is temporally and spatially uniform in the working section.

Bradshaw and Pankhurst (1964) distinguish between unsteadiness and turbulence in temporal uniformity, the difference being somewhat

subjective and dependent on the frequency of variation. Unsteadiness may result from intermittent boundary layer separation in the diffuser due to an excessive expansion angle or too short a contraction section. This may be triggered by an unusually intense turbulent eddy. True turbulence is generated at boundary layers and by the wakes of fan blades, vanes, etc. Lack of spatial uniformity may be caused by poor corner vane design, boundary layer growth and poor fan or straightener vane design causing swirl.

The contraction section and first diffuser both fall within the accepted limits for minimal boundary layer separation. The design of the corners is standard and so would not be expected to contribute greatly to spatial variation. In this tunnel there is no honeycomb although these have frequently been used to counteract swirl and produce directional uniformity (Pope and Harper, 1966). In the absence of any counter-rotating vanes, swirl is minimized by the slow fan tip speed and by the 11 stationary blades downwind of the moving blades. Velocity variation and sound induced by vibrations have been restricted by using a blade ratio of 6 moving to 11 stationary.

An important feature is the sheet of fine wire gauze sited at the windward end of the settling length. This helps to increase uniformity by differential reduction of turbulence and velocity variation. Small eddies produced by the gauze quickly decay in the settling length. The overall increase in velocity which occurs in the contraction section reduces any remaining velocity variation to a small fraction of the average.

6.4 Windspeed control

Windspeed in the tunnel is controlled from a wall-mounted unit

close to the working section. This activates the main motor located near the second corner, the motion of which is translated to the main axial fan by a shaft 1.80m long. The control system is designed to allow continuously variable speeds up to a maximum of 33m s^{-1} to be obtained in the working section.

Variation in the speed of the motor driving the fan may be an important source of temporal variation in the working section. In this tunnel, the speed of the main 15 h.p. d.c. motor (G.E.C. Limited) is accurately regulated by a Stardrive series SRD 20 type E4744 control unit (L.D.E.P. Limited). Control is effected by means of a closed-loop regulator system in which a speed reference voltage is compared with the output voltage from a tacho-generator coupled to the motor. The 'error signal' resulting from this comparison is amplified and used to control the conduction angle of thyristors supplying the motor armature. The thyristors in this 3-phase system only conduct during the positive half-cycles of the a.c. supply and may be triggered at any instant during the half-cycle depending on the error signal. Once triggered into conduction, each thyristor will remain conducting until the a.c. supply completes its positive half-cycle and commences the negative half-cycle. Thus,by advancing or retarding the timing of the firing pulses, the average d.c. output to the armature is increased or decreased.

Despite the elaborate mechanisms for ensuring accurate speed control, it was suspected that there might have been variations resulting from changes in the voltage supply to the building. The reason for this suspicion was the occasional tripping of the reset controls on the compressors.

The works department co-operated in a check of the voltage

supply to the wind tunnel to assess the extent of any sudden surges or voltage variation due to high demand from other equipment in the building. This test showed a normal voltage variation throughout a 24h period of from 225v - 240v. Although there seemed to be no marked surges, it was nevertheless thought that a diurnal variation of 15v might affect the tunnel speed.

This was tested by means of a vane anemometer (Airflow Developments Limited) over a period of several days. Two speeds were used, 2.5m s^{-1} obtained by the centrifugal fan operating alone and 11m s^{-1} with the main fan in operation. The W_1 and W_2 windspeeds used in the yield experiments were obtained by operating the wind tunnel at approximately these settings. At 2.5m s^{-1}, the speed varied by $\pm$0.25% over long periods (several hours) and $\pm$0.75% over short periods. At 11m s^{-1} little variation was observed other than $\pm$1.7% over short periods probably resulting from the passage of an occasional eddy. These results can be regarded as being satisfactory in the case of the centrifugal fan, especially considering that it has no special speed regulation device, and excellent in the case of the main fan. It was, therefore, considered safe to assume that windspeeds would remain constant for long-term experiments.

In July 1968, the spatial variation in the working section was checked by T.E.M. Engineering Limited. In measurements to within 7.5 cm of the walls and ceiling, and along the centre line at positions 51 cm forward or aft of the centre point, they found that, at speeds of 15.24m s^{-1} and 30.49m s^{-1}, the variation did not exceed more than $\pm$0.5% of the mean speed.

6.5 Airflow modification for experimental purposes

This tunnel was designed to have low levels of turbulence and velocity variation in the working section. Although such conditions are certainly unrepresentative of those occurring naturally near the ground, they may be readily modified to suit particular experimental demands.

There are many instances in the literature where attempts have been made to create experimental conditions in which models of, e.g. aeroplanes, stacks, bridges, tall buildings, pedestrian precincts, and shelterbelts may be tested. One of the principles of model testing is dynamic similarity (Shapiro, 1961). This implies equality of certain dimensionless numbers particularly the Froude and Reynolds numbers (Allen and Ditsworth, 1972). If the Reynolds number (Re) is defined as:-

$$R_e = \frac{\text{Density x Speed x Size}}{\text{Viscosity}}$$

it follows that for 2 objects to be dynamically similar, the Reynolds numbers must be equal. In the case of the testing of a small scale model in the wind tunnel, an increase in windspeed may be necessary. This may often involve considerable technical difficulties. Jensen (1958) quoted an example of a house 10m high, exposed to a wind velocity of 40m s^{-1}. Equality of Reynolds numbers based on the product of height and windspeed could have been achieved by the use of a 4m high model with a windspeed of 100m s^{-1}. In the experimental work in this thesis no attempt was made to use models; instead it was intended to realistically represent the wind conditions that a sward of grass might experience in the field.

The relevance of the Reynolds number was questioned by Jensen

(1954 and 1958) since natural air is fully turbulent. Instead, of far more significance for growing plants is the logarithmic velocity profile of natural air which is dependent on the characteristic surface roughness. The growth of a boundary layer characteristic of a particular surface may, however, take a considerable distance to develop. Wind tunnels with good aerodynamic properties inevitably have small working sections in relation to the total size of structure and this means it is rarely possible to develop a full boundary layer. Woodruff and Zingg (1955) achieved considerable success but only by the use of an exceptionally long wind tunnel. Franck (1963) compared various surfaces on a floor of a 12m working section in the Wind Laboratory at the Technical University of Denmark. He found that after 12m, floors of smooth masonite, sand paper, corrugated paper, broken stones and wooden slats produced boundary layers of only 12, 15, 18, 20 and 28 cm thickness respectively.

To circumvent this difficulty many workers have tried to produce turbulent boundary layers by artificial means. Owen and Zienkiewicz (1957), Vickery (1965) and Cowdrey (1967) have used a series of horizontally placed rods at the entrance to the working section. The spaces between the rods were increased vertically according to the gradient of velocity required.

A further refinement was outlined by Counihan (1969); namely the use of elliptical wedges vertically sited up wind of the working section. They considered this a suitable method for simulating a neutral atmospheric boundary layer comparable to that of a rough wall boundary layer.

From the viewpoint of assessing the effect of wind on the growth of grass, modelling of scaled velocity profiles for the testing of large engineering structures is inappropriate; of much greater interest

is the behaviour of the wind at the grass surface, particularly the gustiness, spatial uniformity and turbulence.

No attempt was made to produce gusts in this wind tunnel although the idea would certainly merit further work.

Spatial variation in velocity may be due to the development of a velocity profile over the grass along the working section. This is inevitable and wind tunnels with short working sections seldom allow space for sufficient plant material to be discarded in the cause of profile development. To decrease this difficulty, it was decided to use an artificial material, placed at the end of the contraction section, to present a leading edge to the wind and also to develop a profile. In this way, the whole of the working section could be used for experimental material.

Chamberlain (1966) in wind tunnel studies to measure the vertical flux of a gas to grass used, as one of his surfaces, an artificial grass made from P.V.C. strips, stuck on a substrate of sealing wax. The strips were 8 cm long, 0.5 cm wide and 0.025 cm thick. They projected 7.5 cm above the wax and equal numbers were orientated edge on, face on and in each of the directions making 45^{0} to the direction of wind flow. The average density was one strip per 1.8 cm^{2} of wax.

Thom (1971), in a study on the absorption of momentum by vegetation, used an artificial crop constructed from rigid circular cylinders, 0.1 cm in diameter, planted firmly in an expanded polystyrene substrate. The cylinders, one per square cm, were assembled in a diagonal pattern to form crop units 30 cm-square. These units could then be built up to form a crop. The final height of the crop was 14.3 cm.

Dr.A.S.Thom kindly lent 3 of his units to be used as a leading edge for experimental material. Before installation, they were mounted

on hardboard to give extra support for securing them to the tunnel floor.

It was noticed that whilst growing plants under such conditions, leaf flutter seemed restricted; there was a tendency for leaves to bend over and then remain essentially stationary. Under natural conditions, the higher levels of turbulence and velocity variation produce frequent leaf flutter. It was therefore decided to increase the levels of turbulence in the working section by vortex generation from cylinders.

The patterns of vortex generation have long been of interest to workers in fluid dynamics. Homann (1936) (in Schlichting, 1960) has visually shown the nature of the vortices and their variation over a range of Reynolds numbers.

In the measurements described below, vortices were created in the working section by the use of two 12.5 cm diameter cylinders placed in the contraction section, one horizontally and the other vertically. By unscrewing an extendible foot from a wood plate secured within each cylinder, sufficient pressure could be exerted against the tunnel walls to ensure that each was firmly supported. To increase light reflection each cylinder was covered in silver-coated polyester.

The cylinder Reynolds numbers based on diameter as the representative length were high for all windspeeds of interest experimentally. Therefore the vortices produced would have decayed rapidly so that even the grass nearest to the cylinders (5 diameters distant) would have experienced a highly turbulent air flow. Also since 2 cylinders were used, there would have been considerable interaction between the vortices produced. The use of relatively large cylinders ensured correspondingly large eddies and also that the decay of turbulent energy would not be too rapid.

The arrangements for growing plants in the working section are shown in Plates 6.1 and 6.2.

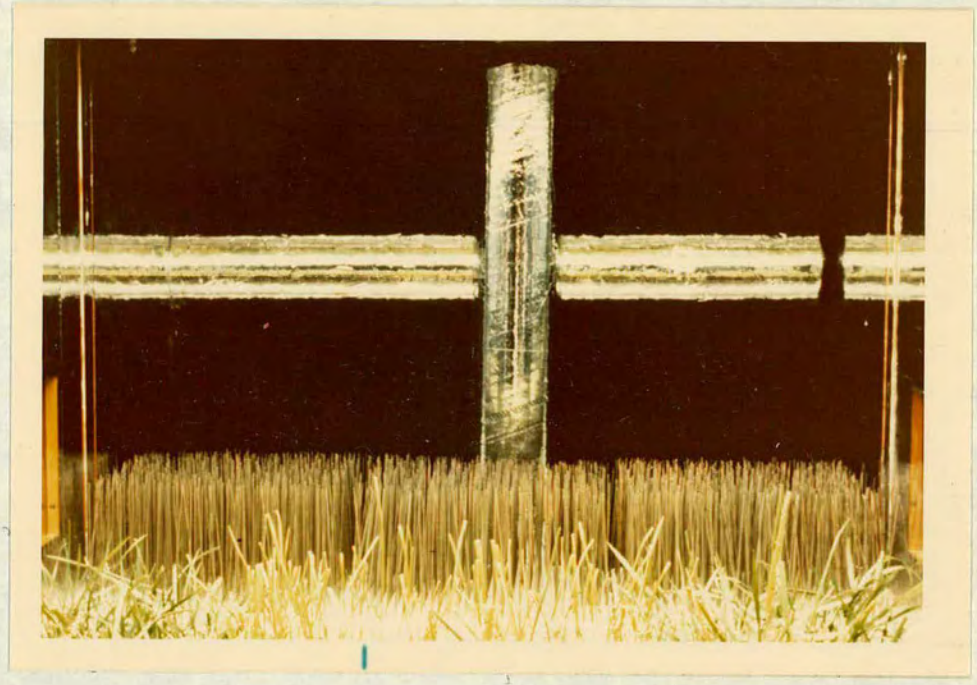


Plate 6.1 View of the working section from inside the first diffuser showing experimental plants of S.170 Festuca arundinacea, the artificial crop and the turbulence generators.

Plate 6.2 View of the working section, when lowered, showing the arrangement of boxes containing experimental plants of S.170 Festuca arundinacea.

6.6 Instruments for velocity and turbulence measurement

A number of instruments were used for measuring velocity during the experimental period. As a standard instrument for measurements at a point, a 0.30m pitot static tube (Airflow Developments Ltd.) was used. The velocity may be calculated from the difference between the static and total pressure heads by the formula:

$$P_t - P_s = \tfrac{1}{2}\rho v^2$$

where P_t = Total pressure

P_s = Static pressure

ρ = Density of air

v = Velocity

This instrument was always used for precise determinations of tunnel speed. The sensitivity of pitot tubes to errors from yaw (Bradshaw, 1969) and the provision that differences between the velocities at the points of measurement along the tube should ideally be nil, restrict the use of this method of measurement to conditions of low turbulence.

The pressure difference was measured by a model 513 micro-projection manometer (T.E.M. Ltd.). It is claimed that this has the ease of operation of a standard Betz Manometer but, although manufactured to a high standard, it was found to have serious limitations especially for use at low windspeeds. In particular, it was found that the speed of response was very slow and the scale often stuck, usually not at all obviously. At low velocities, pressure differences are in any case very small and difficult to detect. A type 503 Industrial Manometer (Airflow Developments Ltd.) was later installed and this was found to have a much faster response time and to be much more sensitive to the low windspeeds encountered by crops close t

the ground.

For rapid measurements of velocity, a type RM-137 Electronic Anemometer (Airflow Developments Ltd.) proved to be particularly useful. This comprises a vane anemometer and a transistorized indicator unit. Mounted on the outer ring of the vane assembly is a small housing containing a capacitance transducer so arranged that, as the vanes rotate, a succession of electrical impulses are developed and fed to a rate meter operating a scale. Four scales are available giving full scale deflections at 1, 2.5, 10 and 25m s^{-1}. An output signal, giving a 1 milliamp full scale deflection over each velocity range with an accuracy of 1%, provided a means by which velocities in the tunnel could be recorded. The signal was connected via a 100 ohm resistor to an Electronik 19 potentiometric recorder (Honeywell Ltd.) allowing records to be taken over long periods. As the anemometer head is 11.5 cm in diameter, its use in confined areas is limited.

Of much greater use for small scale measurements in the vicinity of a crop was the mini-vane anemometer (Schiltknecht Ltd.) which works on a similar principle. The anemometer head in this case is only 2.0 cm in diameter. The output is displayed on one of three scales having full scale deflections of 1, 2 and 6m s^{-1}.

For simultaneous measurement of velocity and turbulence, Dr.J.Morgan of the Department of Civil Engineering and Building Science kindly lent his hot-wire measuring system. This consisted of a DISA Type 55F31 hot-wire miniature probe coupled to a DISA Type 55D05 constant temperature anemometer. The signal from the anemometer was linearized by a DISA Type 55D15 linearizer before being used to display the instantaneous velocity as a d.c. voltage on a model L.M. 1619

digital voltmeter (Solartron Ltd.) and the root mean square values on a type 612A true R.M.S. voltmeter (Dawes Ltd.).

At very low windspeeds, the use of hot-wire anemometers is limited by buoyant convection. Collis and Williams (in Bradshaw, 1971) note that this may be neglected if the Reynolds number is greater than the cube root of the Grashof number, the ratio of a typical buoyant force to a typical viscous force. For the hot-wire used, the Grasshof number is about 6×10^{-6} which means that only at lower velocities than about $0.05 m\ s^{-1}$ is buoyant convection likely to be a problem. All windspeeds measured in the tunnel were in excess of this.

The hot-wire probe used in all measurements was connected by a probe holder and standard 5m cable to the anemometer. The wire itself was made from 5 μm diameter platinum plated tungsten. The combined resistance at $20^{o}C$ of probe and cable was 4.1 or 4.0 ohms of which the cable accounted for 0.7 ohms.

Considerable care is required in the calibration of the hot-wire system. The precise procedure is outlined in the DISA instruction manual. The calibration is specific for a particular probe at specific overheating ratios, temperatures and windspeed ranges. In all measurements the probes were operated at a 10:1 bridge ratio and a resistance setting of 6.2 ohms to give a suitable overheating ratio. The coil adjustment governing the frequency response of the anemometer was checked on each occasion by means of an oscilloscope and a square-wave generator.

The procedure for linearizing the output from the anemometer is also described in the DISA instruction manual. By adjusting the controls on the linearizer, values can be assigned to the various constants of a fairly complex transfer function. Of particular

importance is the $\frac{\text{minimum input voltage}}{\text{maximum output voltage}}$ % which was set at the maximum value of 57-76% throughout. Also important is the selection of exponent which depends on the range of velocities of interest. Usually for velocities in the range of 3-200m s^{-1} exponent 3 is selected but for the lower range of velocities exponent 2 is more suitable.

The suitability of using exponent 2 was however tested by comparing the two exponents over a range of relevant velocities to assess which gave the most effective linearization. In this test, a pitot static tube was used as a standard instrument. This was placed in a central position at the windward end of the working section at a height of 30 cm and the hot-wire probe placed at the same height about 10 cm distant. Care was taken to ensure that there was no interference from the production of wakes and also to minimize any support structures in the vicinity of the probes themselves. The tunnel speed was adjusted to provide a range of from 4m s^{-1} to 12m s^{-1} and the outputs compared for the two exponent values.

The results showed a rather curvi linear response with exponent 2 at the higher velocities, whilst exponent 3 was more linear throughout. For operation at low velocities, it was clear that an extrapolation of the output line using exponent 2 approached the origin at zero velocity far more closely. To ensure greater accuracy at low velocities, exponent 2 was used on all occasions.

Under experimental conditions, the values shown on the two voltmeters were subject to considerable fluctuation which created problems in assessing the average readings. The output on the digital voltmeter was observed for one minute and the extreme values noted and then averaged. With the R.M.S. voltmeter, movement of the needle was

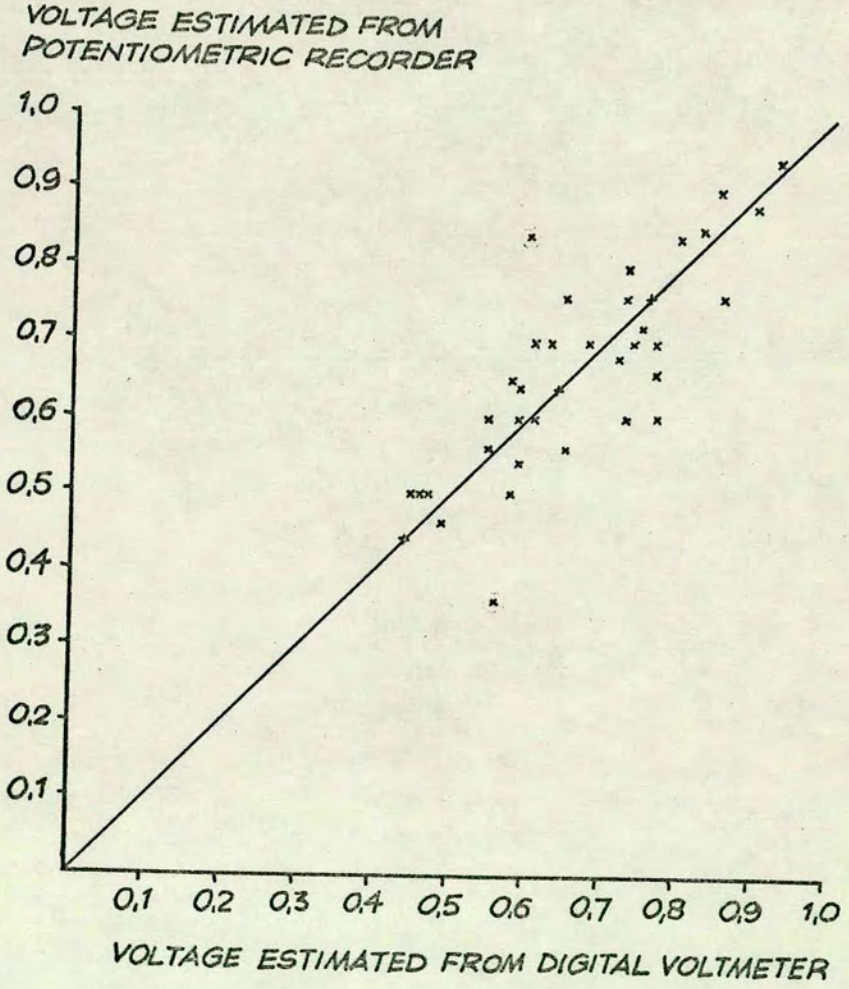
observed and an 'average' value noted. Calibration of the R.M.S. voltmeter had previously been checked by a type J2E A.F. signal generator (Advance Electronics Ltd.).

A check on the validity of this method of velocity measurement was made by connecting an output from the digital voltmeter to a Honeywell Electronik 19 potentiometric recorder and the average velocity assessed from the highly erratic recorder trace. To do this, a low wind speed had to be used, namely 2.5m s^{-1}, the W_1 windspeed of the wind tunnel yield experiments. To have used higher speeds would have produced such a violently erratic response from the recorder as to be highly detrimental to its continued use. In such situations,a means by which oscillations in the output signal from the digital voltmeter could be damped would need to be developed. The relationship between the values obtained by the two methods is shown in Figure 6.2 where a perfect agreement should indicate a straight line of unit slope. The values were in sufficient agreement as to place confidence in the original method of velocity measurement.

6.7 Measurements of velocity and turbulence in the working section

In this series of measurements, the tunnel speed was set at 7m s^{-1} and the effects on velocity and turbulence of the various modifications of airflow assessed. Measurements were also taken with a grass crop in position at a growth stage comparable with that normally reached about half way through a yield experiment. Such experiments are fully described in later chapters. During all measurements, the temperature was maintained at $5^{o}C$ since the response of the hot-wire anemometer is dependent on ambient temperatures. The small size of the probe made it ideal for measurements within or near the grass canopy but, due to its extreme delicacy, it was found very difficult to avoid breakages

FIGURE 6.2
COMPARISON OF VOLTAGE ESTIMATES FROM SOLARTRON DIGITAL VOLTMETER AND FROM HONEYWELL 19 POTENTIOMETRIC RECORDER.



caused by contacts with grass blades.

In calibrating the anemometer for a full-scale deflection of 7m s^{-1}, (Figure 6.3), the problem arose of measuring wind speeds less than 4m s^{-1}. The pitot tube and manometer were very insensitive at such speeds since 4m s^{-1} corresponds to a pressure difference of approximately 1 mm water gauge. Also, this was the minimum windspeed possible in the unobstructed tunnel with the main fan in operation. Acording to accepted practice, any values at low velocities were obtained by extrapolation of the linearized output. It was not possible to evaluate the effectiveness of the linearization at such low velocities or whether the output at zero velocity passed through the origin. For these particular readings, most values measured were not much below 4m s^{-1} and so readings obtained by extrapolation could be treated with confidence.

With the velocity in the working section set at 7m s^{-1}, the velocity around the cylinders was found to be 7.25m s^{-1}. The cylinder Reynolds number (Re) was calculated as:

$$Re = \frac{\text{diameter x velocity}}{\text{kinematic viscosity}} \text{ (at } 10^{o}C)$$

$$= \frac{0.125 \text{ m x } 7.25\text{m s}^{-1}}{0.00001437\text{m}^2 \text{ s}^{-1}}$$

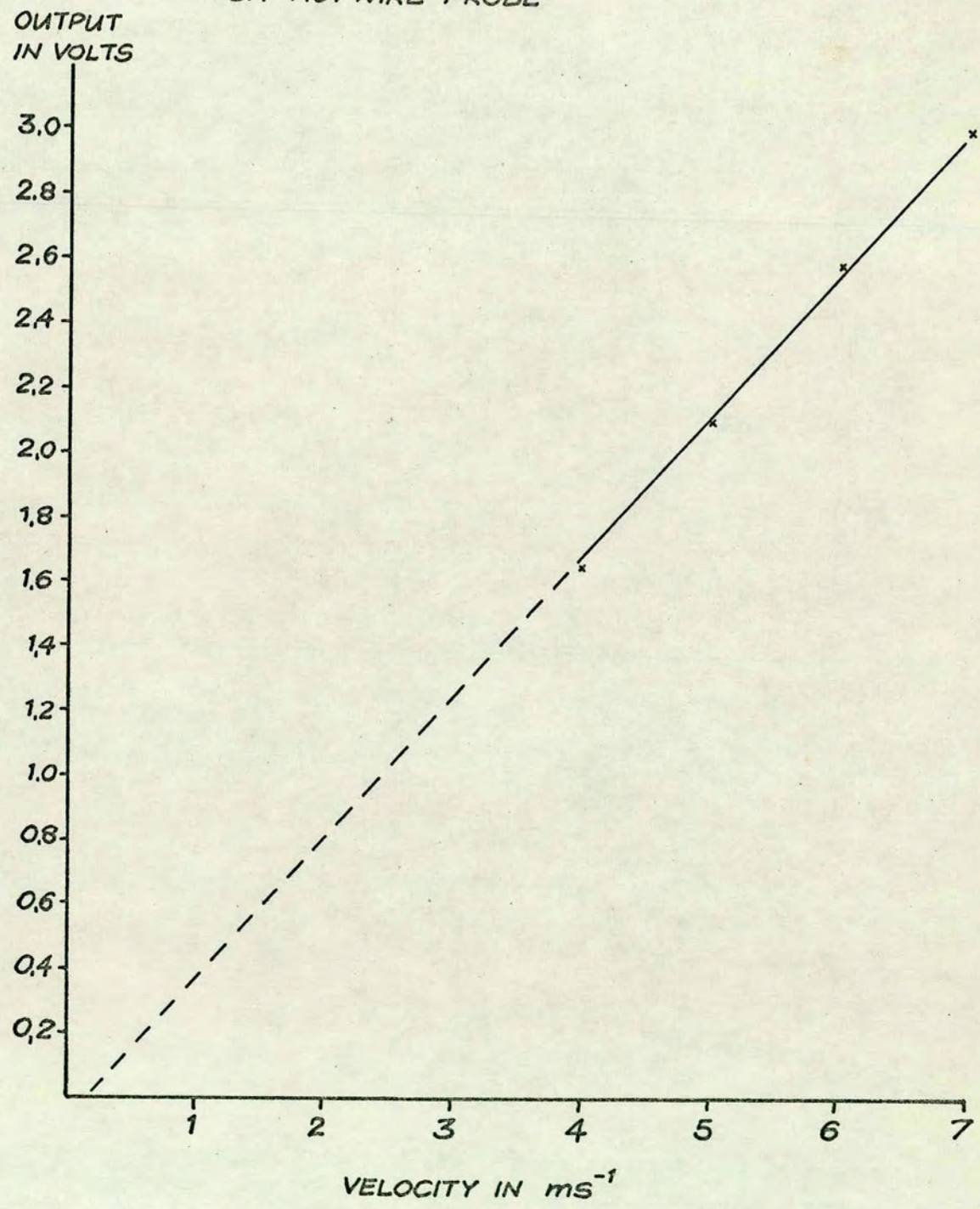
$$= 63065$$

At such a high Reynolds number the value of the Strouhal number was taken at 0.210. The frequency of vortex shedding (f) was calculated as:

$$f = \frac{0.210 \text{ x } 7.25\text{m s}^{-1}}{0.125\text{m}}$$

$$= 12.18\text{s}^{-1}$$

FIGURE 6,3
CALIBRATION OF
DISA HOT-WIRE PROBE



As stated previously, the vortices so produced would rapidly have become fully turbulent.

In experiments to be described later, 20 boxes containing grass, each 30 cm long x 21 cm wide x 15 cm deep fully occupied the floor of the working section. A position corresponding to the centre of each box was then taken as a measuring point regardless of whether a box was actually present. In the absence of boxes, the floor of the working section was covered by a wooden sheet which was continuous with the base of the contraction section and on which the 20 positions were marked. The probe, whether supported on a board or centrally in each box, remained at the same height in relation to the air flow, i.e. at a height of 25 cm. When placed in boxes containing the growing crop, the height of the probe was level with the tallest of the grass blades. under windy conditions, the canopy became deformed so that the probe projected about 9 cm above crop height. It was considered that, in the interests of minimizing wire breakage, this was the closest distance possible. In taking the measurements, care was taken to ensure that the supporting structure for the probe did not interfere with the readings obtained. Each time the probe was repositioned,care was taken to minimize error from yaw.

The two values obtained were used to calculate the percentage turbulence as follows:

$$\% \text{ Turbulence} = \frac{\text{R.M.S. voltage}}{\text{D.C. voltage}} \times 100$$

6.8 Results of hot-wire velocity and turbulence measurements

In the following paragraphs, the velocity and percentage turbulence readings were noted for the 20 positions under each set of conditions. A plan of the measurement positions,which also corresponds to the box positions in later experiments, is shown in Figure 6.4.

FIGURE 6.4
PLAN OF POSITIONS IN THE WORKING SECTION

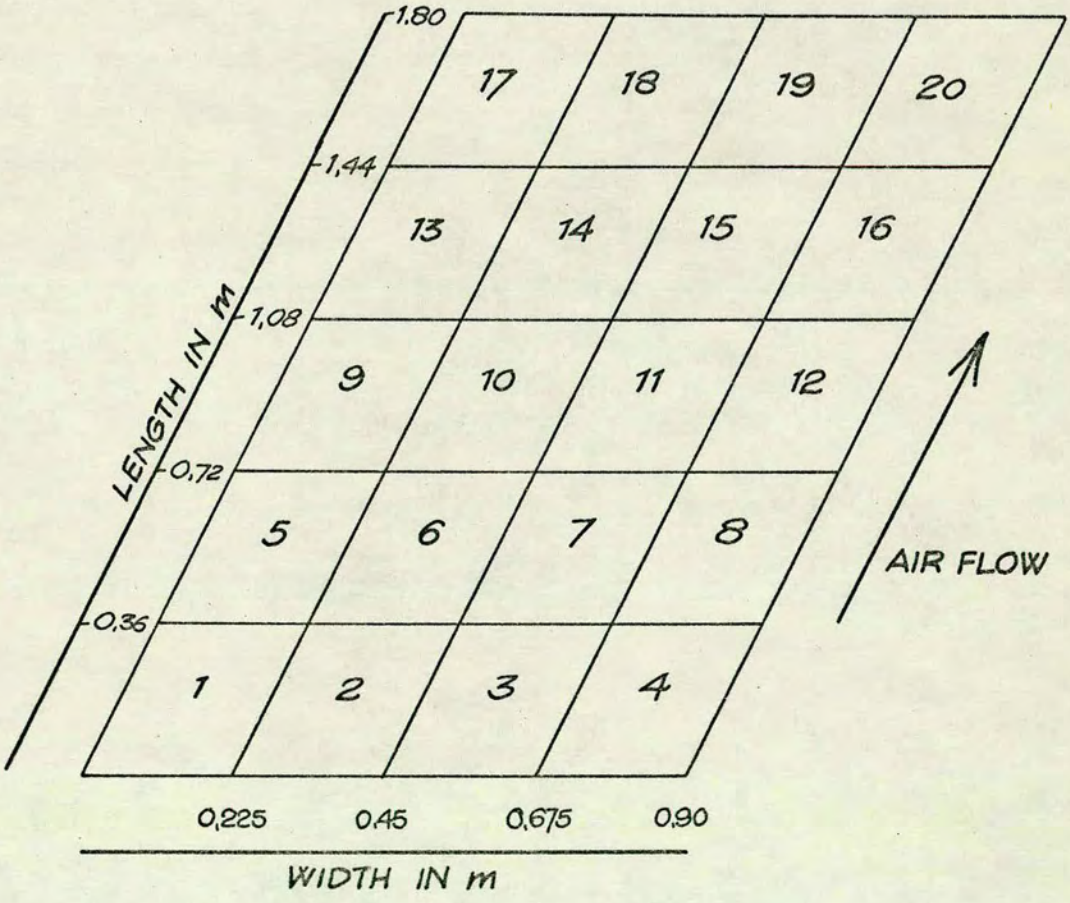
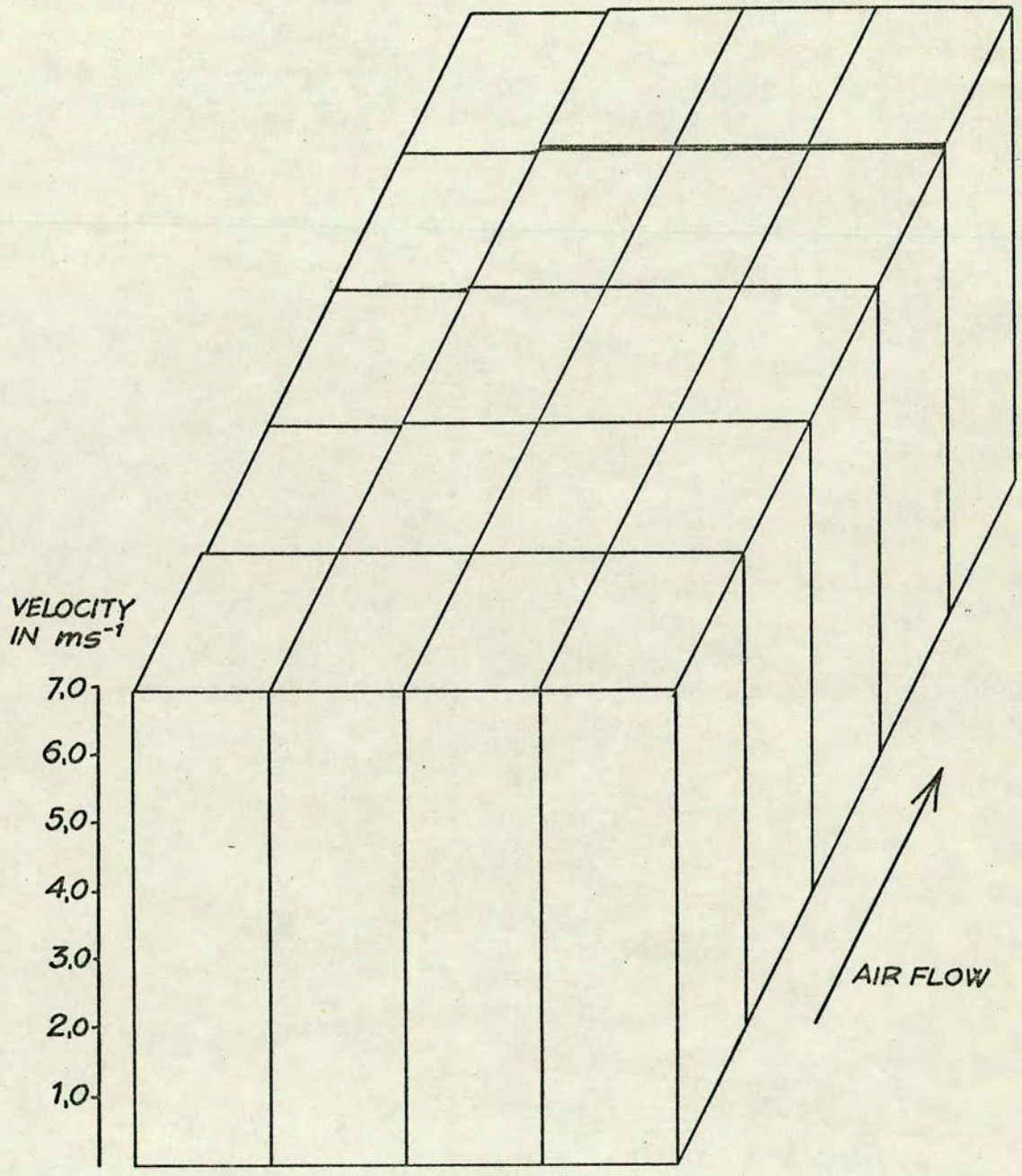
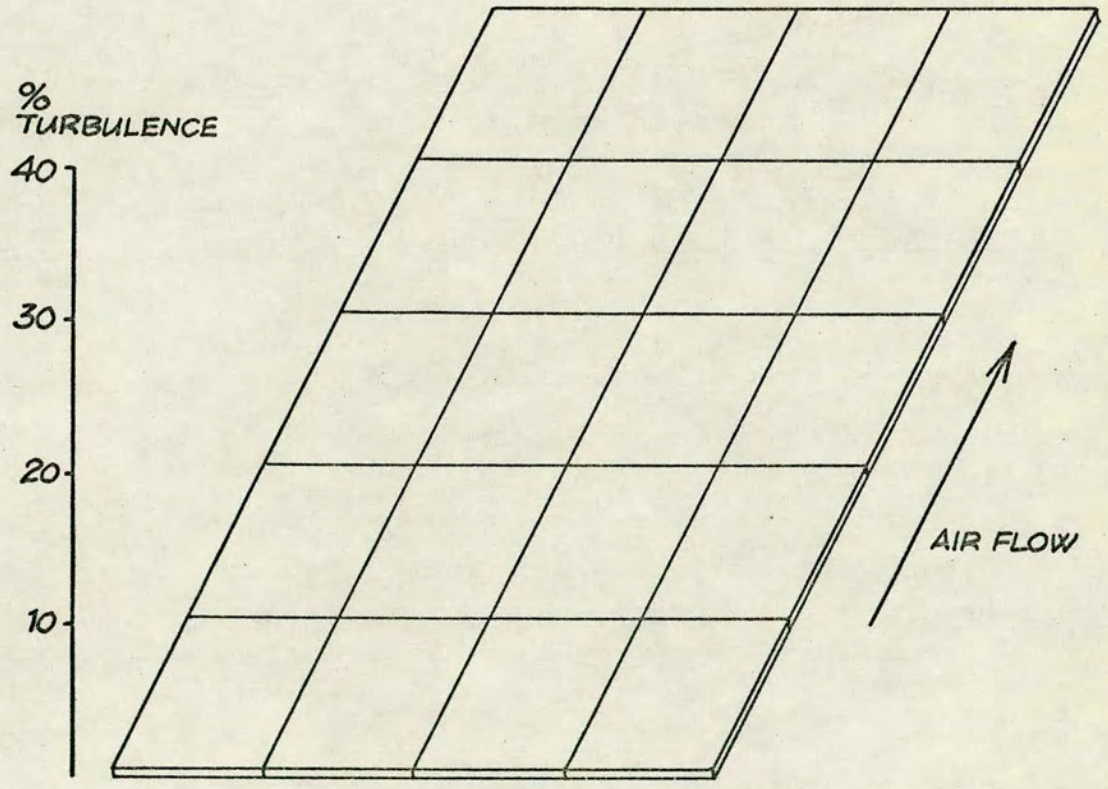


FIGURE 6.5
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25 m HEIGHT



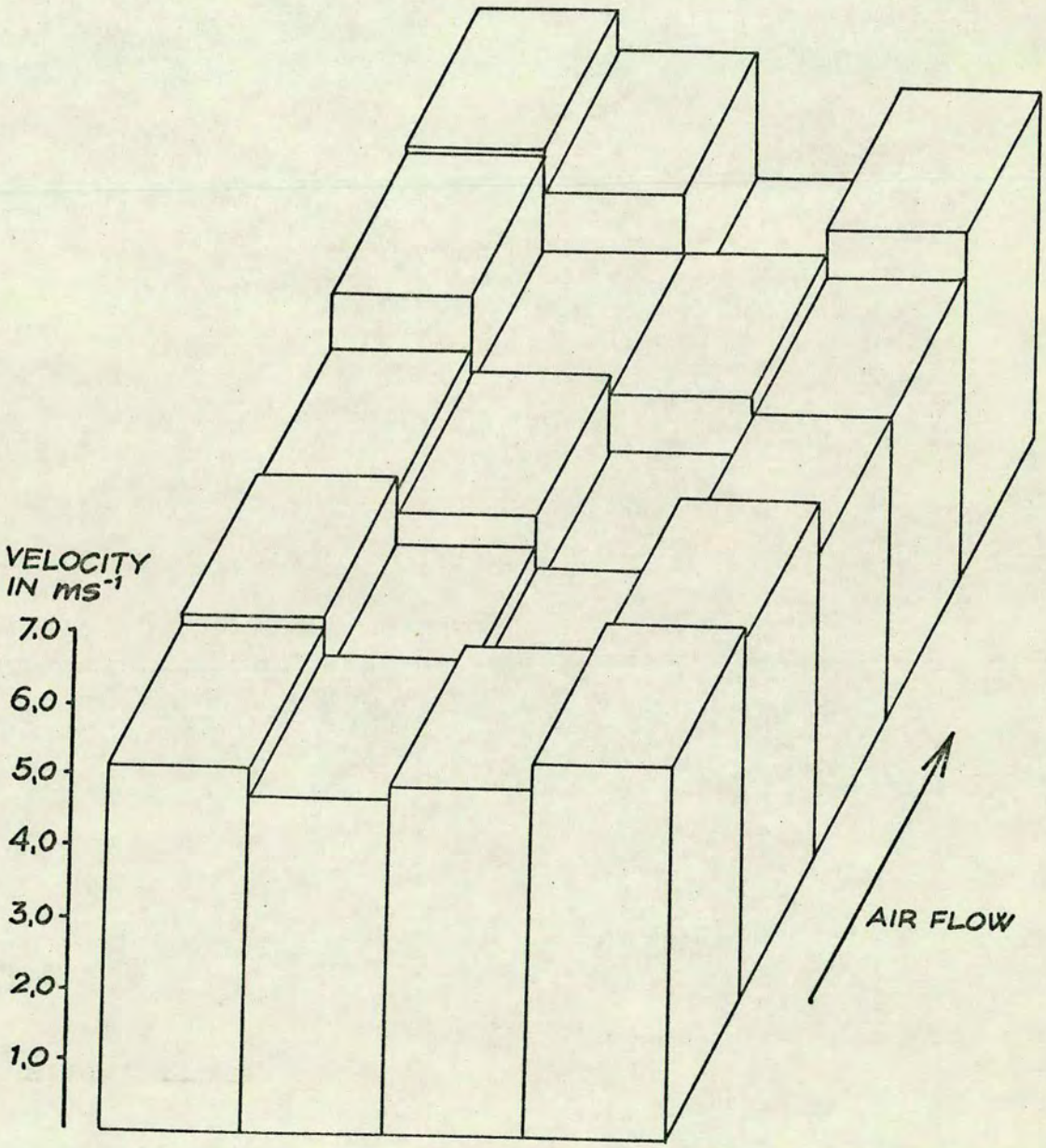
CONDITIONS : Velocity : 7ms^{-1}
Tunnel unobstructed

FIGURE 6,6
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25 m HEIGHT



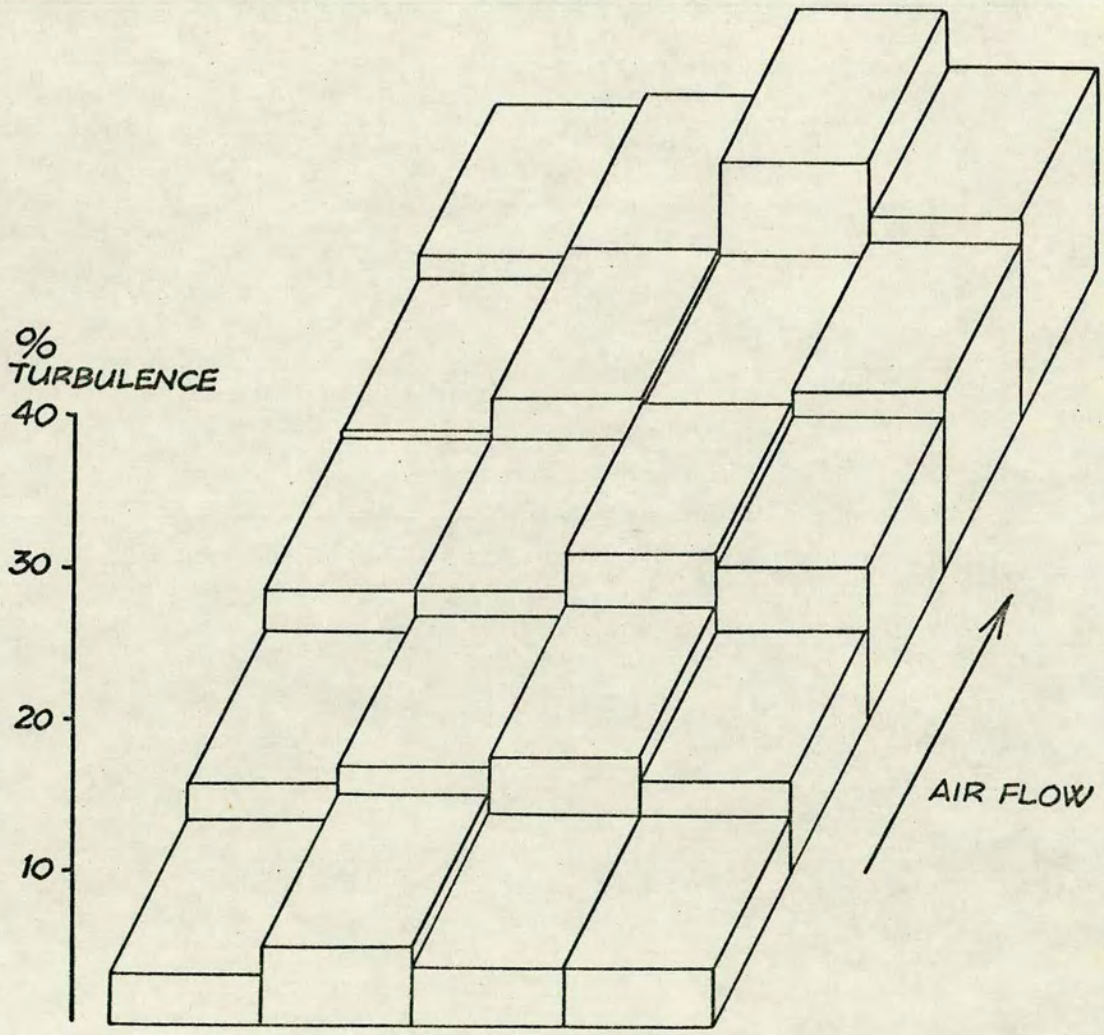
CONDITIONS : Velocity : 7 ms^{-1}
Tunnel unobstructed

FIGURE 6,7
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25 m HEIGHT



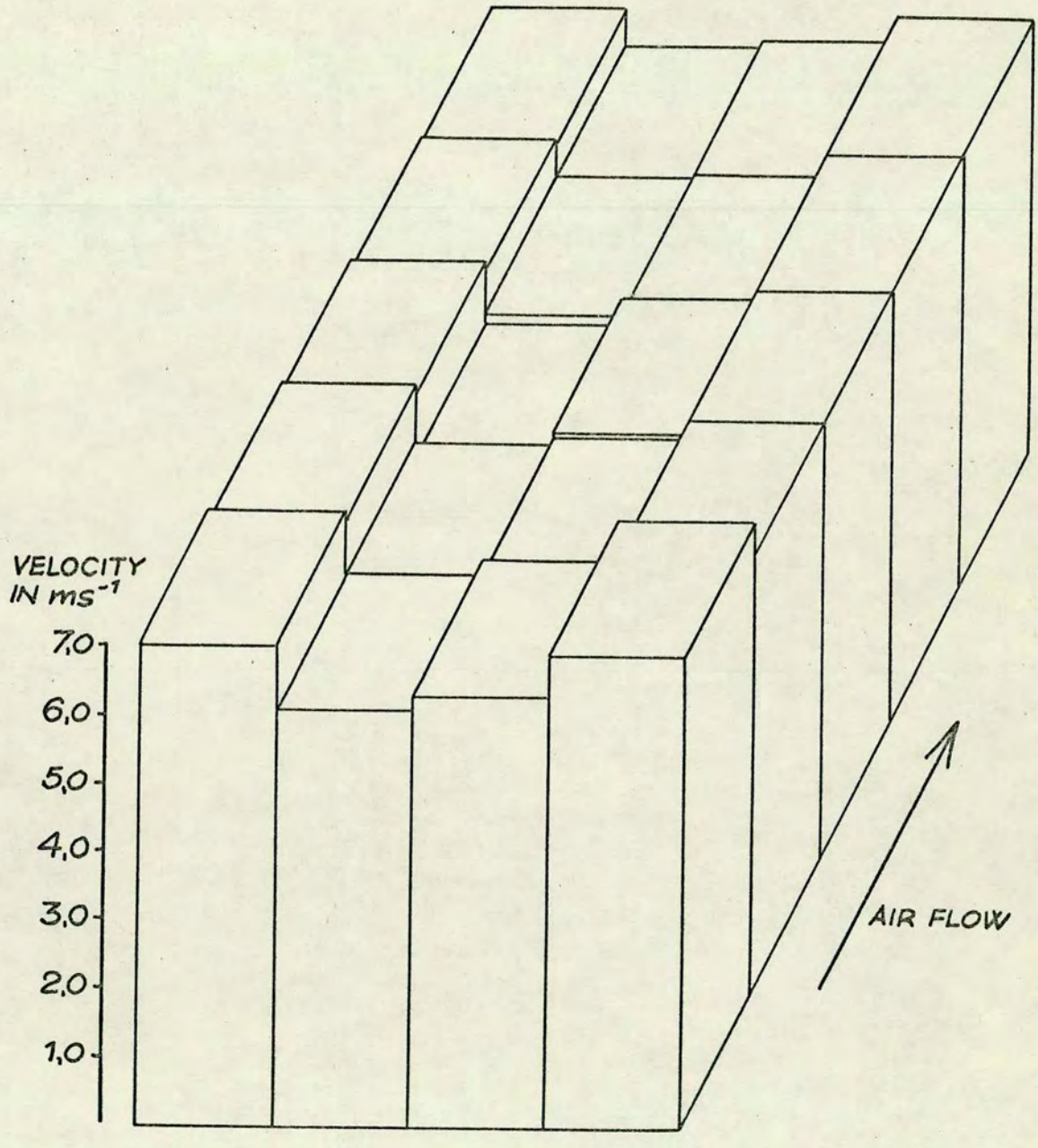
CONDITIONS : Velocity 7 ms^{-1}
+ Artificial crop

FIGURE 6,8
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25 m HEIGHT



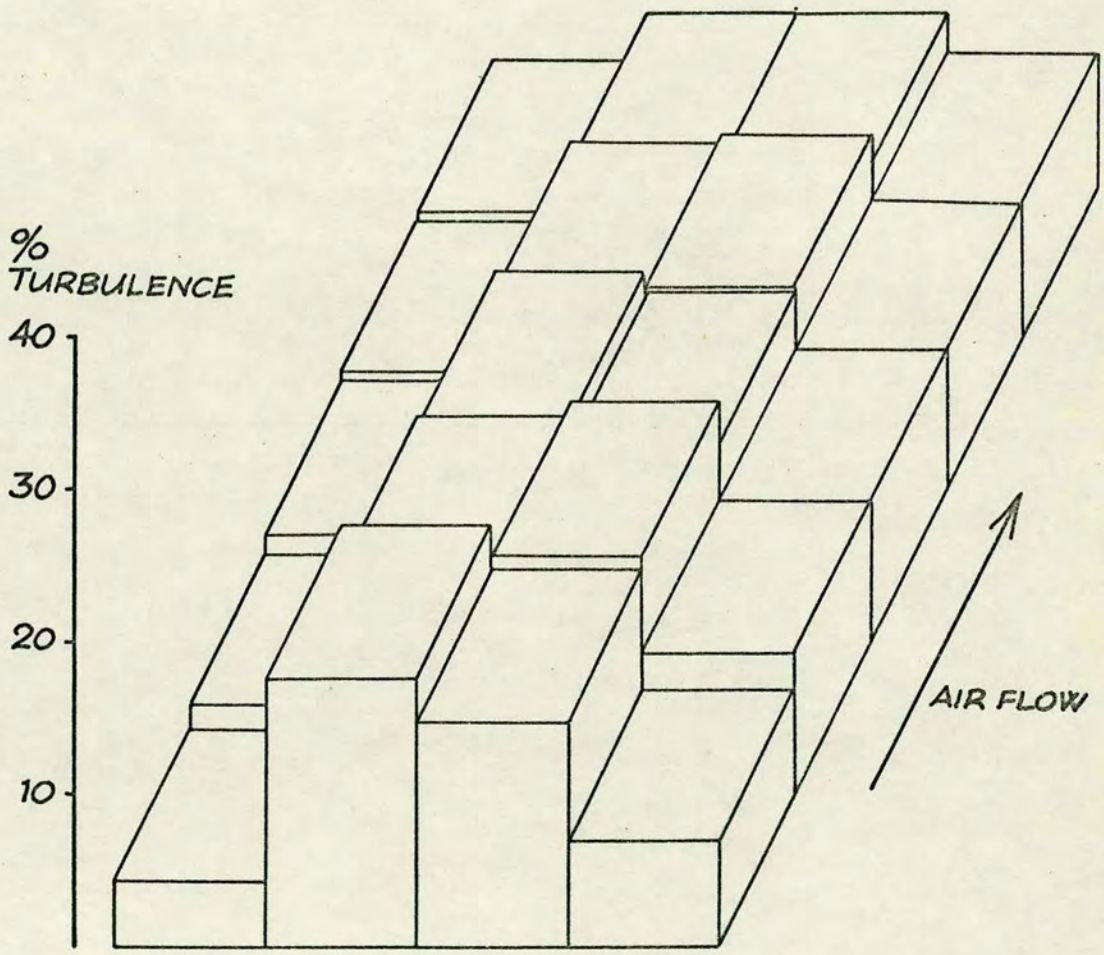
CONDITIONS : Velocity : 7 ms^{-1}
+ Artificial crop

FIGURE 6,9
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25 m HEIGHT



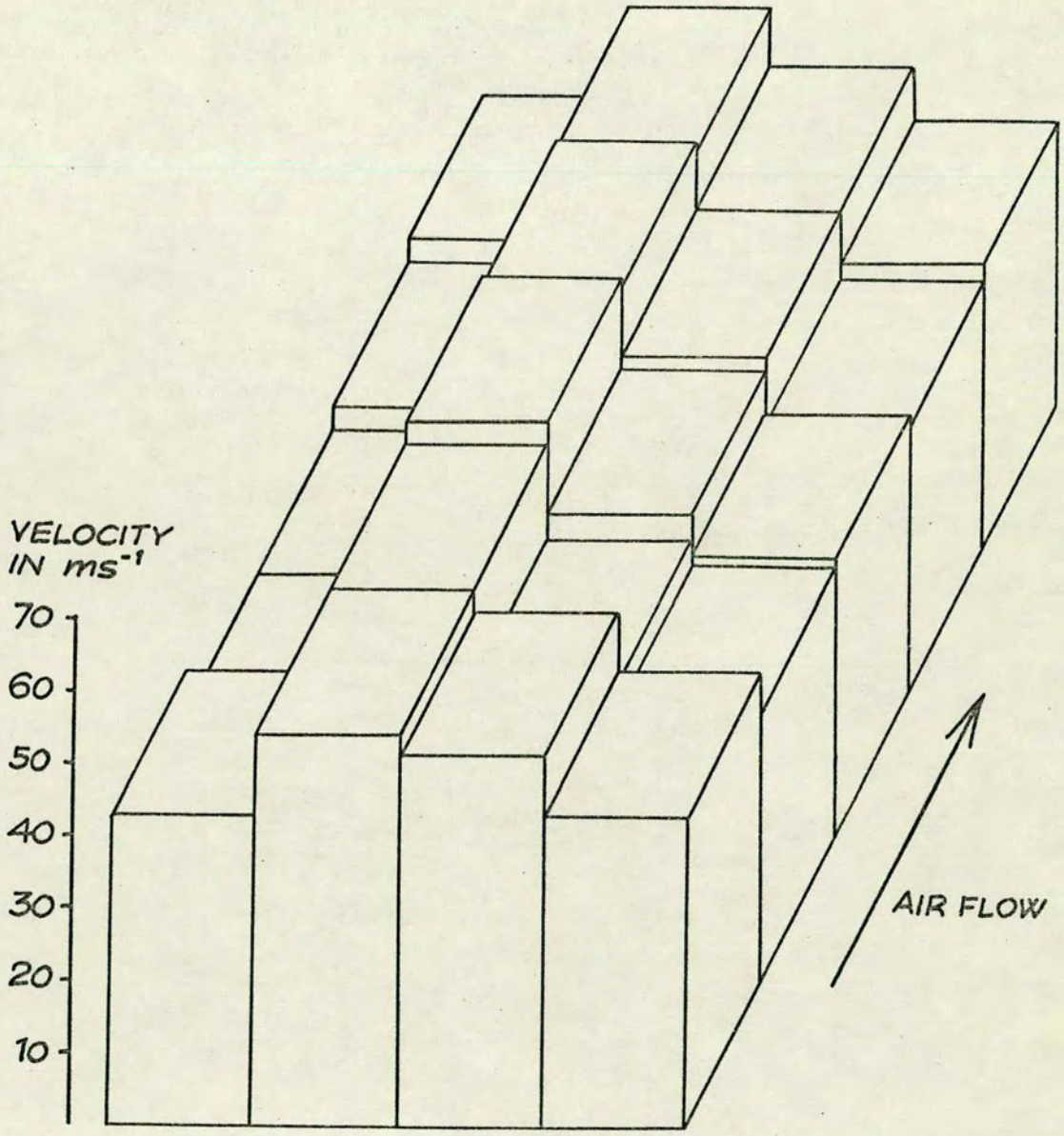
CONDITIONS : Velocity : 7 ms^{-1}
+ Turbulence generators

FIGURE 6,10
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25 m HEIGHT



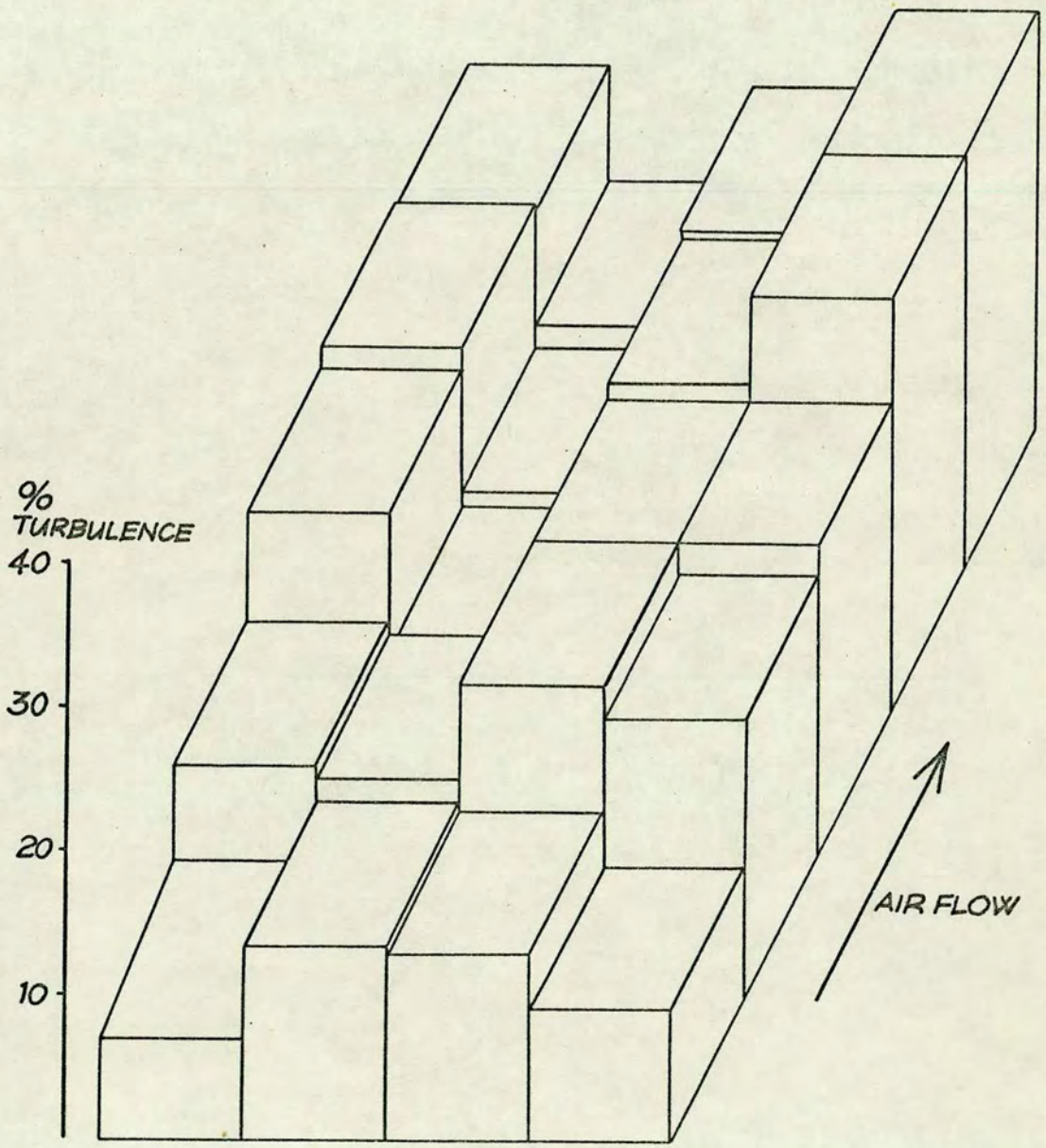
CONDITIONS : Velocity : 7 ms^{-1}
+ Turbulence generators

FIGURE 6,11
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25 m HEIGHT



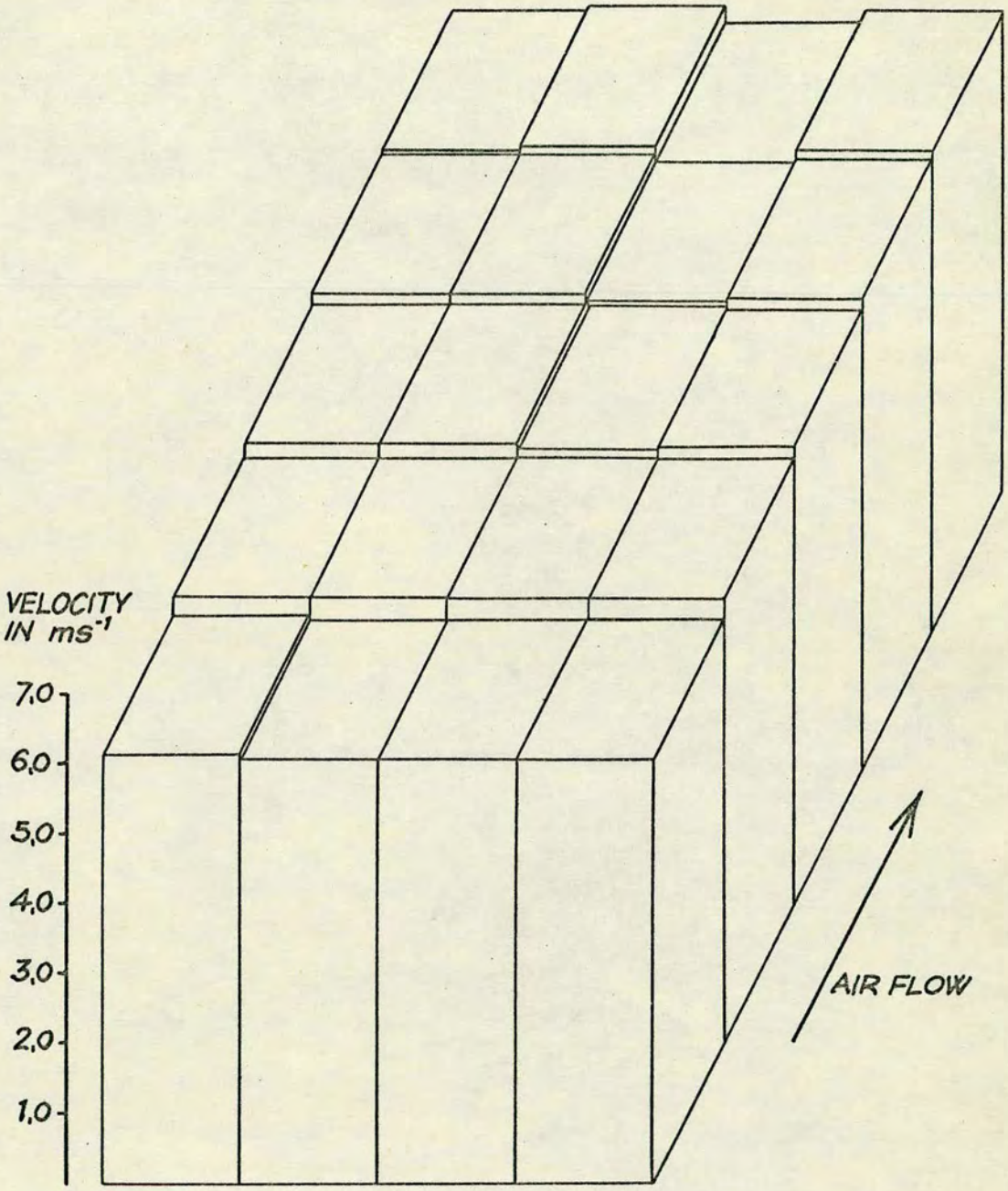
CONDITIONS : Velocity : 7 ms^{-1}
+ Artificial crop
+ Turbulence generators

FIGURE 6,12
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25m HEIGHT



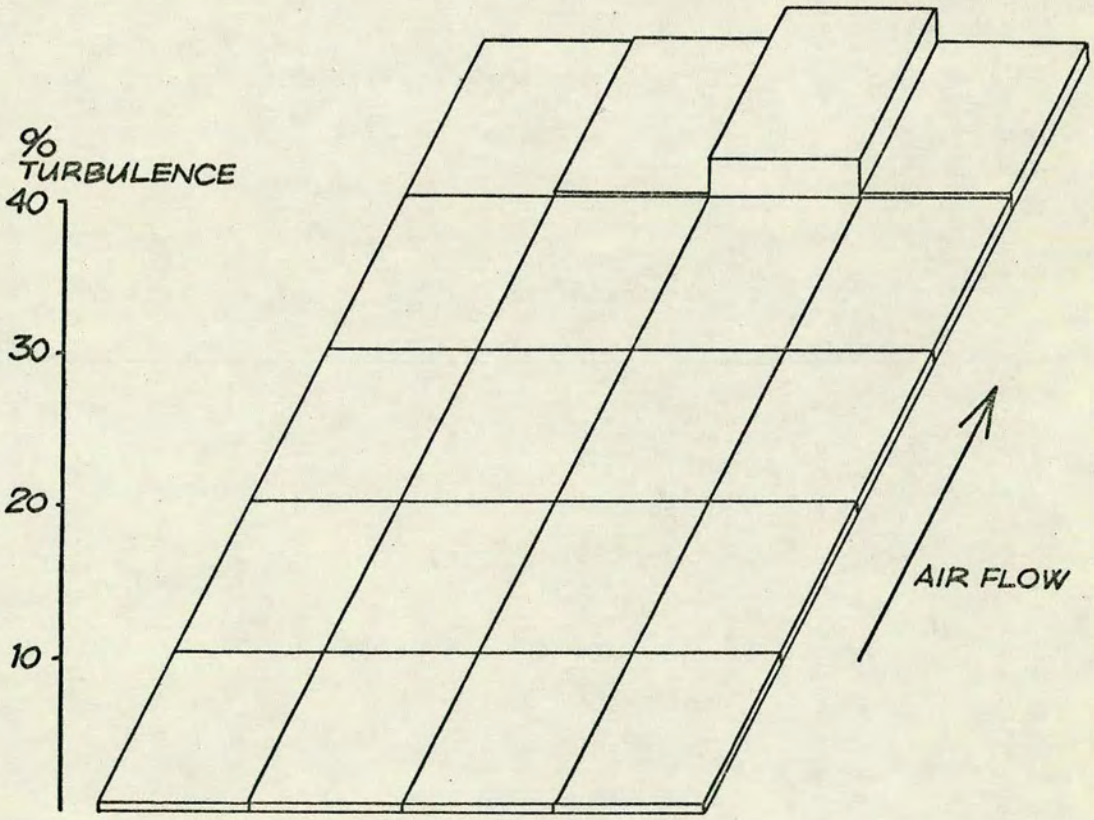
CONDITIONS : Velocity 7 ms^{-1}
+ Artificial crop
+ Turbulence

FIGURE 6,13
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25m HEIGHT



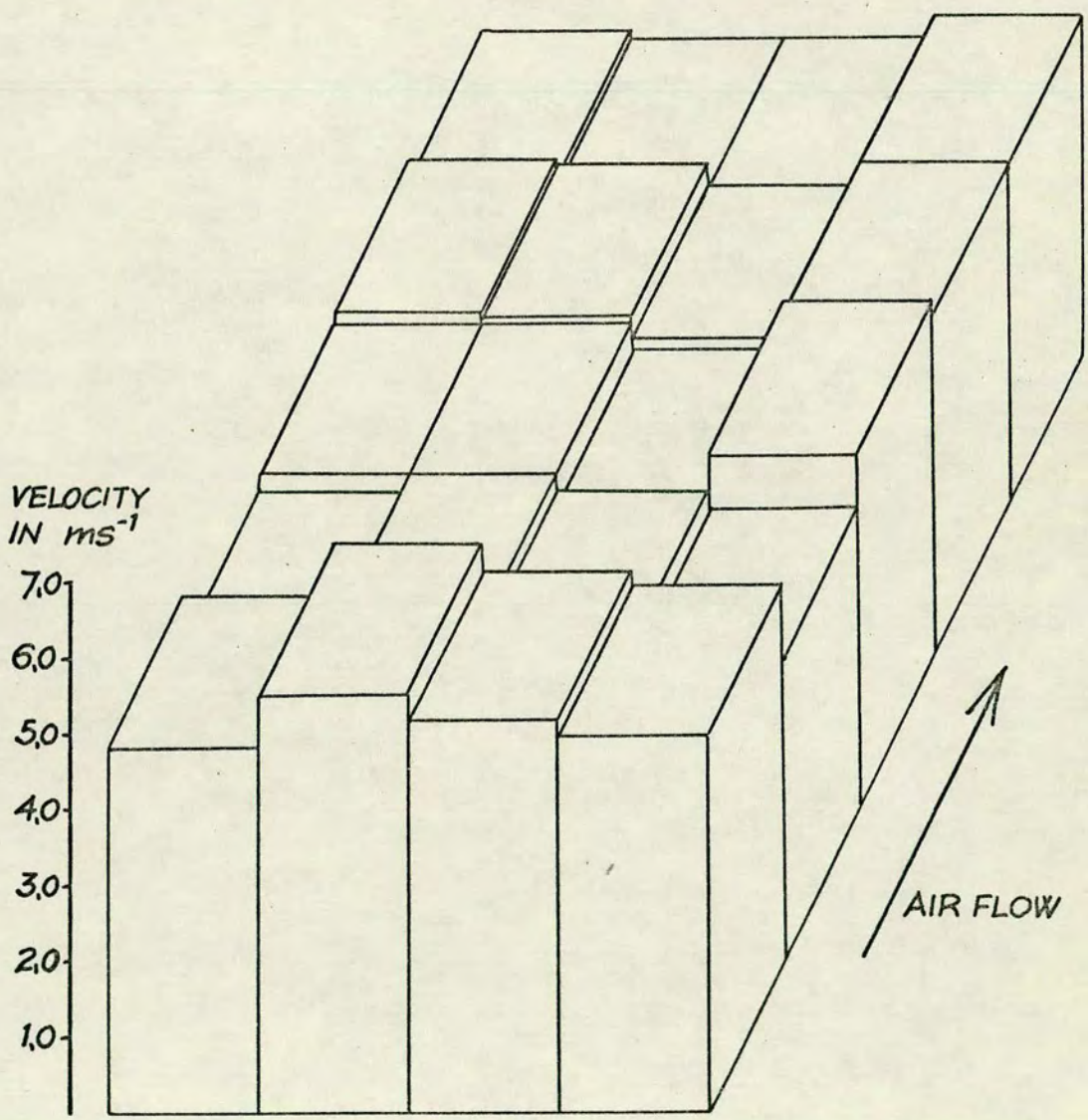
CONDITIONS : Velocity 7 ms^{-1}
+ Grass crop alone

FIGURE 6,14
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25m HEIGHT



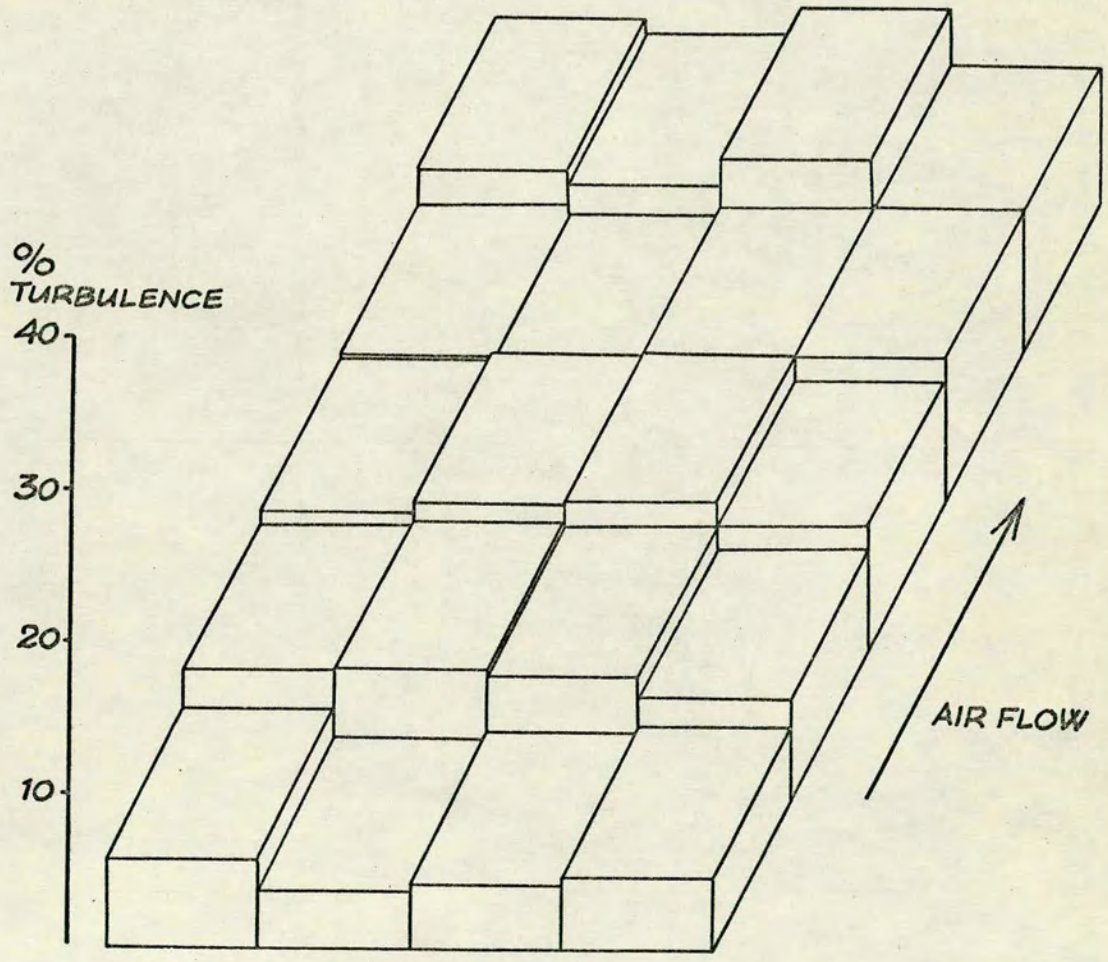
CONDITIONS : Velocity : 7 ms^{-1}
+ Grass crop alone

FIGURE 6,15
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25 m HEIGHT



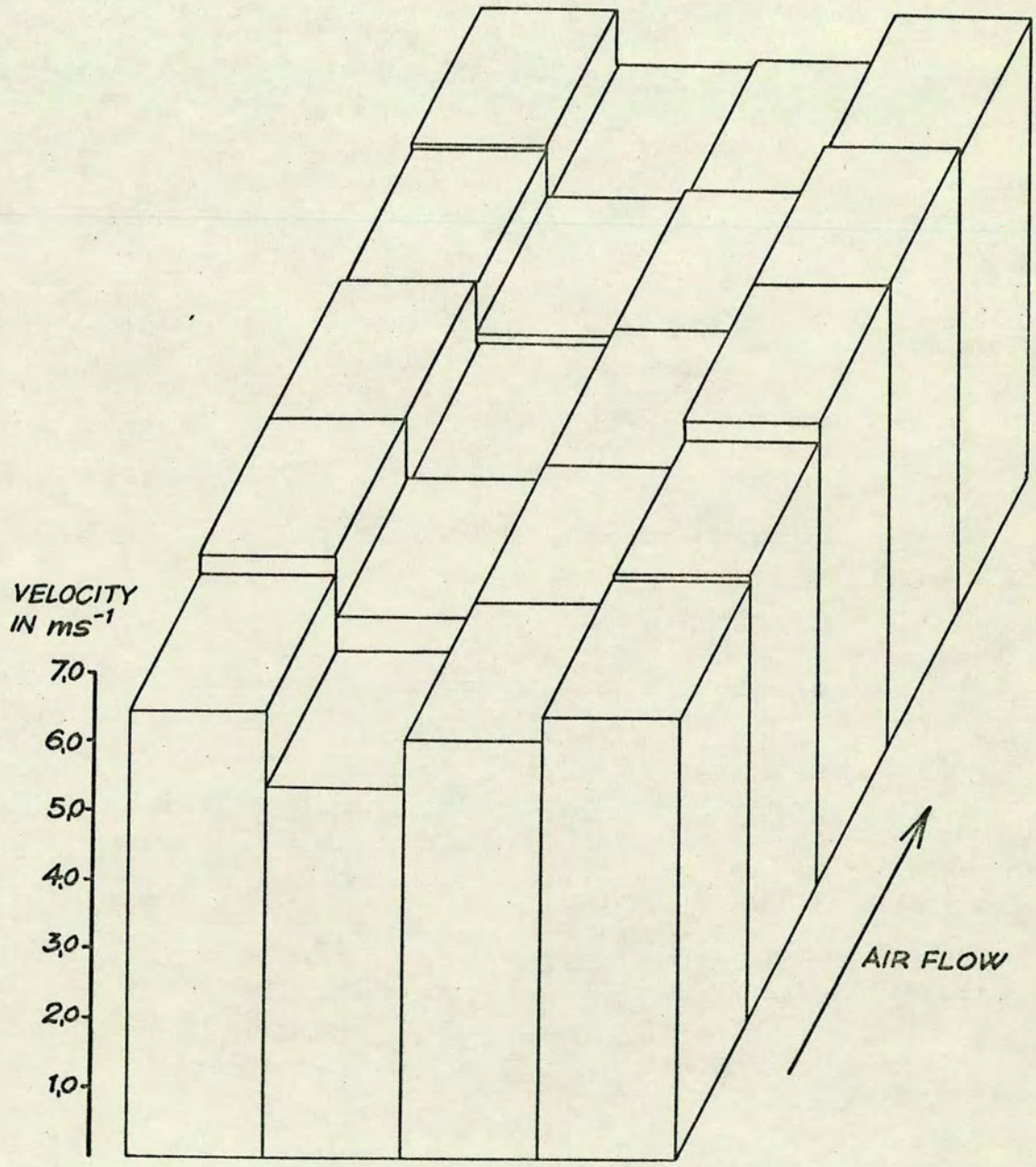
CONDITIONS : Velocity : 7 ms^{-1}
+Grass crop
+Artificial crop

FIGURE 6,16
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25 m HEIGHT



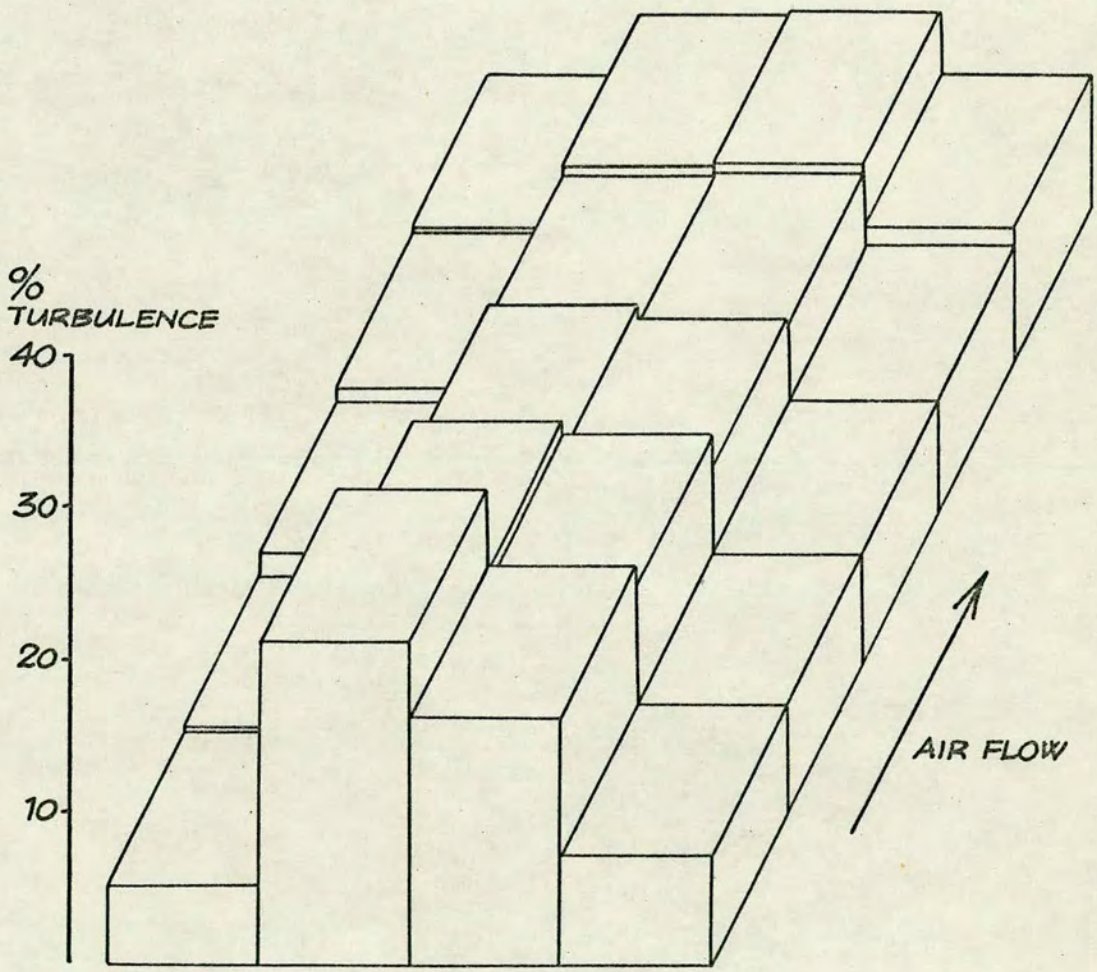
CONDITIONS : Velocity 7 ms^{-1}
+ Grass crop
+ Artificial crop

FIGURE 6.17
WORKING SECTION
VELOCITY DISTRIBUTION AT 0.25 m HEIGHT .



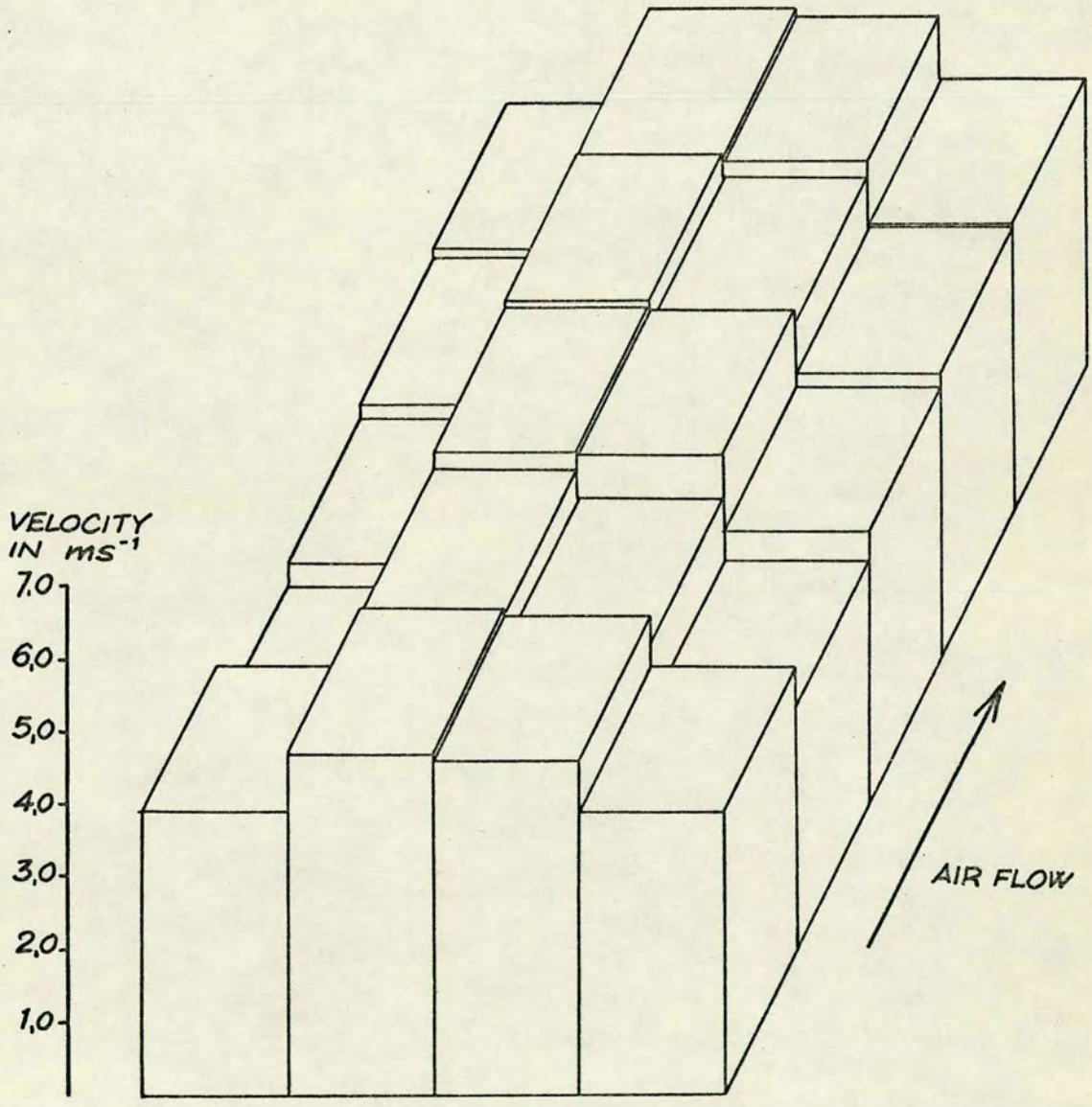
CONDITIONS : Velocity : 7 ms^{-1}
+ Grass crop
+ Turbulence generators

FIGURE 6,18
WORKING SECTION
% TURBULENCE DISTRIBUTION AT 0,25 m HEIGHT



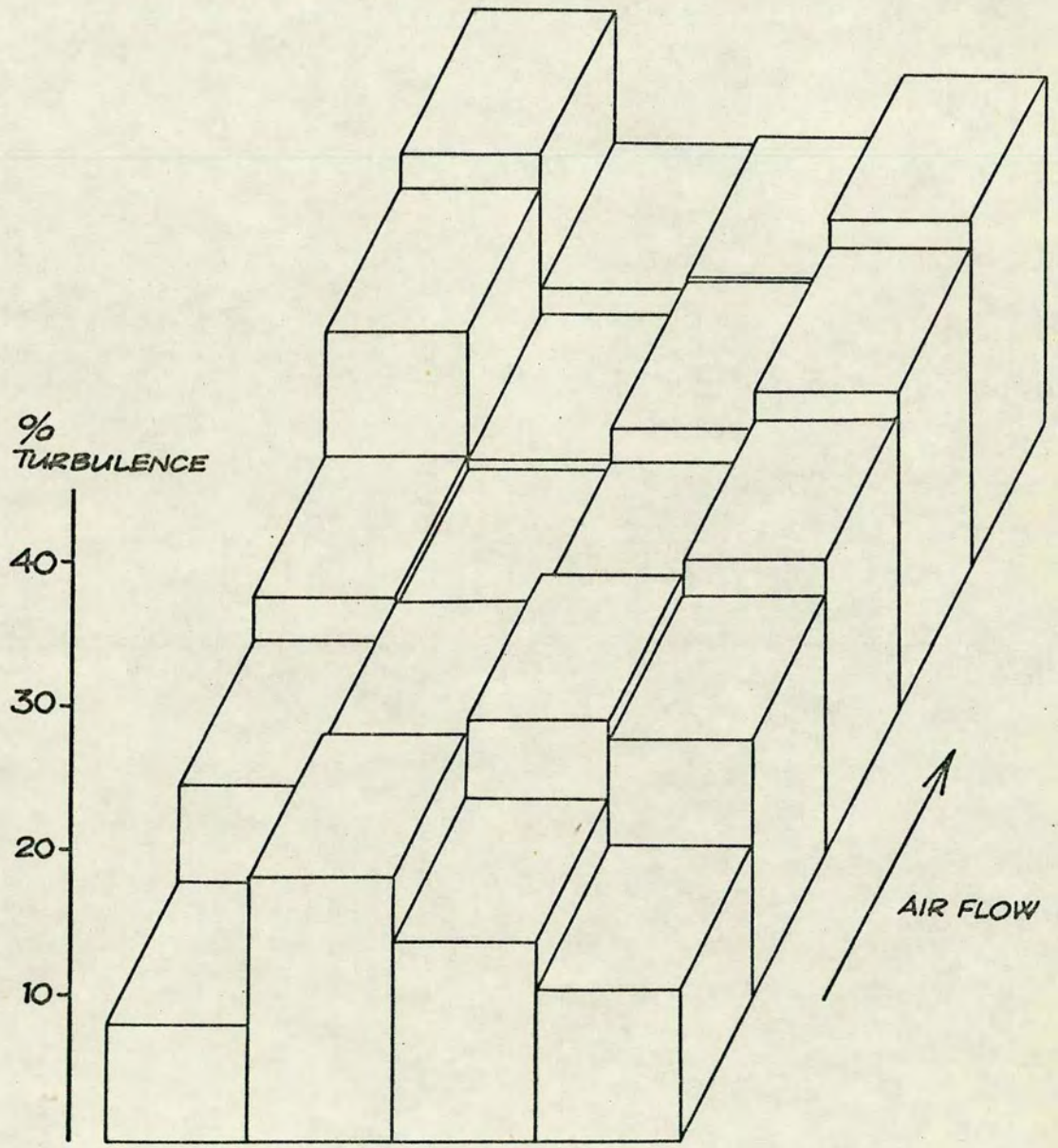
CONDITIONS : Velocity : 7 ms^{-1}
+ Grass crop
+ Turbulence generators

FIGURE 6.19
WORKING SECTION
VELOCITY DISTRIBUTION AT 0,25 m HEIGHT



CONDITIONS : Velocity 7 ms^{-1}
+ Grass crop
+ Artificial crop
+ Turbulence generators

FIGURE 6.20
WORKING SECTION % TURBULENCE
DISTRIBUTION AT 0.25 m HEIGHT



CONDITIONS : Velocity : 7 ms^{-1}
+ Grass crop
+ Artificial crop
+ Turbulence generators

In measurements in the unobstructed tunnel (Figures 6.5 and 6.6), the high spatial uniformity was clearly apparent. At no position was the turbulence greater than 0.53%, illustrating the high quality of the tunnel design.

Using the artificial crop as a leading edge (Figures 6.7 and 6.8) produced a considerable reduction in velocity and increase in turbulence. The peculiarly low velocity at position 19, associated with the highest turbulence value of 16.67%, was not simply due to a higher R.M.S. voltage which was only 250 mV. Figures 6.7 and 6.8 suggest also, that the artificial crop was acting rather like an over-dense shelterbelt producing a strongly sheltered area followed by an area of high turbulence (Caborn, 1957).

With the turbulence generators acting alone (Figures 6.9 and 6.10), there was a less marked reduction in velocity but a clear increase in turbulence especially in the central positions, perhaps associated with the wake from the vertical cylinder. Downstream, there was a decrease in turbulence centrally but an increase peripherally suggesting turbulent energy exchange. The highest level of turbulence was 15.7%.

With both the artificial crop and turbulence generators in position (Figures 6.11 and 6.12), there was a marked increase in the amount and positional variation of turbulence. The maximum value was 28.75%. Further overall reductions in velocity also occurred.

The same sequence of measurements was then repeated with a grass crop in position. With the working section unobstructed (Figures 6.13 and 6.14), there was little noticeable effect of the grass crop. The crop itself showed severe canopy deformation at the leading edge, a feature which decreased steadily downwind associated with the growth of the boundary layer. The velocity increased downwind and, although not apparent from turbulence measurements, the increased leaf flutter

would suggest that turbulence also increased. It seems that the probe was probably too high to have been affected by the presence of the crop.

Similar patterns as previously observed without grass, were obtained by the introduction of the artificial crop (Figures 6.15 and 6.16). However, grass appeared to reduce the variation in velocity, the upwind positions being higher and the downwind positions being lower (cf. Figure 6.7). The high level of turbulence previously noted at position 19 was also apparent under these conditions.

The introduction of the turbulence generators (Figures 6.17 and 6.18) again reduced velocity and raised turbulence in the central positions associated with the wake from the vertical cylinder. The maximum level of turbulence was 21.24%. Again, there was a tendency for turbulence to decline centrally and increase peripherally along the working section.

The combination of the grass crop, the artificial crop and the turbulence generators raised the turbulence level to 28.48% (Figures 6.19 and 6.20). This situation is of interest since it was similar to that used in yield experiment 4, the most comprehensive of the yield experiments. There was a rapid rise in the percentage turbulence along the 2 outer rows of boxes not attributable to a decrease in velocity. The percentage turbulence tended to be higher in the central positions at the windward end, but since it remained fairly constant along the working section, it was comparatively lower at the leeward end.

It is clear that the use of the artificial crop as a leading edge and the cylinders as turbulence generators both fulfilled their intended functions. A point considered important for future experi-

ments was the very large spatial variation resulting from these modifications to the air flow. Such variations might have been expected to affect yields and a method of frequent randomizing was therefore developed.

6.9 Lighting conditions in the working section

For purposes of growing plants and illuminating the working section, a bank of twenty-four warm white fluorescent tubes was provided by the manufacturer to a design specification of 29160 lux. Despite efforts to improve the intensity and the distribution of the irradiance on the floor of the working section, both aspects remained far from ideal. T.E.M. Engineering Limited attempted to improve the distribution by erecting mirrors external to the working section in the hope of reducing the loss of radiation to the exterior. Thus, radiation having passed through three layers of 0.6 cm plate glass would be reflected back again, doubtless with considerable reflective and refractive loss. It was decided, instead, to line the working section internally with highly reflective silver-coated polyester which, because of its thickness and smooth surface, would not be expected to contribute to the growth of the boundary layer.

An investigation into the possibilities of replacing the single bank lighting system by a double bank showed such a scheme to be prohibitively expensive. The heat build-up would have demanded the installation of a cooling system with ducting to the exterior of the building. In the absence of any cooling system for the single bank already in existence, the light output was reduced by an excessive build-up of heat. The optimum operation temperature for maximum output from a normal fluorescent tube is about $40^{o}C$. The tubes when lit

were too hot to touch and so their operating temperature would have been about 60-70^{o} C. This is similar to the optimum operation temperature of the recently produced amalgam tubes and so twenty-one 80W white amalgam tubes (Thorn Lighting Ltd.) were installed. After stabilization, the increase in irradiance due to using amalgam tubes amounted to 20%.

The full complement of 24 tubes was made up by the addition of 3 radar red tubes. These tubes have a very high output at 6650 $\mathring{A}$ and since this is a wave band of strong Chlorophyll A absorption, it was thought that these tubes might be useful to enhance plant growth.

The spectral composition of the wind tunnel lighting as finally used for experiments was measured by a spectro-radiometer (Spectro-systems Ltd.) and the results shown in Figure 6.21.

A detailed measurement of the light distribution on the floor of the working section by use of a photocell (Evans Electroselenium Ltd.) showed a large and disturbing variation despite the use of the silver-coated polyester. Readings were taken after the intensity had stabilized at sixty 15 x 15 cm square positions, an area which in total approximated that later occupied by all the experimental boxes. The results are shown in Table 6.1 where the readings are expressed as a percentage of the highest values obtained from the centre of the working section. The peripheral values fell to about 60% of those measured centrally and clearly such a serious variation provided further justification for frequent randomizing in future experiments.

The values of the radiation on the floor of the working section were reasonably realistic for the conditions experienced by plants in spring in southern Scotland, and so were quite suitable for the practical implications of the work in this thesis. An accurate

FIGURE 6.21 SPECTRAL COMPOSITION OF FLUORESCENT TUBES IN WIND TUNNEL WORKING SECTION MEASURED BY A SPECTRORADIOMETER

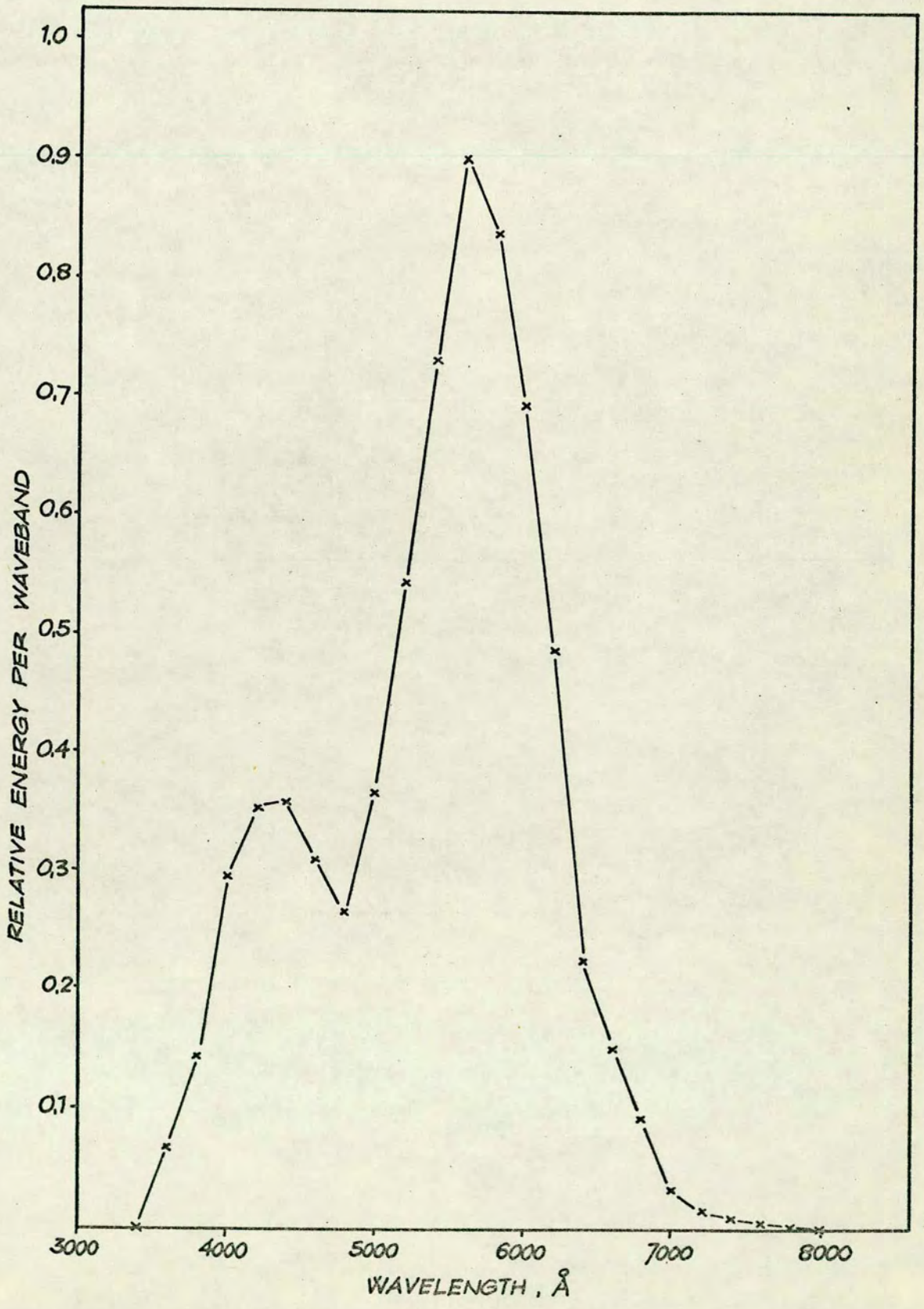


Table 6.1 Relative illumination on the floor of the working section (%).

Distance from inside edge(cm)	Distance from leeward end (cm) 7.5	22.5	37.5	52.5	67.5	82.5	97.5	112.5	127.5	142.5
7.5	57	67	76	81	83	83	81	74	69	60
22.5	62	76	83	90	95	95	90	83	74	62
37.5	67	83	88	95	100	100	95	88	79	67
52.5	67	81	90	98	100	100	98	90	79	67
67.5	64	76	88	95	98	98	95	88	79	67
82.5	60	71	81	86	88	88	86	81	71	62

measurement of the absolute values was carried out by means of a solarimeter (Kipp and Zonen Ltd.) connected to a potentiometer. This was placed at 9 positions, those used for velocity checks in later experiments. The solarimeter was calibrated at the Kew Gardens Observatory in June 1969 and had an output of 0.0123 mV W m^{-2}. The mean value for the 9 readings was 48.3W m^{-2}.

6.10 Air Conditioning

The activation of the components of the air conditioning system is in response to the primary sensors, a Sangamo-Weston 376700-14 resistance bulb thermometer and a Honeywell type Q 457 A hygrometer.

The temperature element projects downwards from a central position in the roof of the tunnel at the front of the first diffuser and allows temperature control of $\pm$ 0.5^{o} C.

The humidity element is sited in the centre of the left vertical wall (relative to the direction of air flow) of the first diffuser. A shaped wooden block serves to streamline the element and, to preserve symmetry, an identically shaped dummy is mounted in the opposite wall. The unit itself contains a bank of humidity - sensitive elements connected to form a resistance network. The elements themselves are plastic and each is lined with 2 gold leaf grids coated with lithium chloride. Temperature compensation is provided by a resistance thermometer bulb housed within the unit. Such a unit may be expected to give an accuracy of $\pm$ 2% relative humidity but may be subject to ageing. This was checked after 3 years and shown to be negligible.

The primary sensors are connected to separate Honeywell 'Electronic 15' circular chart controllers coupled with Honeywell 'Electr -O- line' positioning control units. Such units, when correctly

adjusted, allow for practically straight line control of temperature and relative humidity at desired settings. Essentially acting as a potentiometer, this system allows for the comparison of an input signal, proportional to either temperature or relative humidity, with a signal corresponding to the setting on the circular chart recorder. The difference between the 2 voltages, constituting an error signal, is amplified and then drives a balancing motor which simultaneously repositions the chart indicator. The resistance of a slidewire is simultaneously adjusted thus changing the feed-back voltage until, eventually, the feed-back and input voltages become equalized at which point the circular chart will correctly indicate conditions inside the working section.

In a similar manner, an amplified error signal drives a Honeywell M 934A modutrol motor which re-positions a contactor on the slidewire changing the feed-back voltage until the error signal is reduced to zero.

The modutrol motor is connected by means of a short shaft to a Honeywell S435 Step Controller containing a series of 10 micro switches. These are sequentially operated by the action of the Modutrol motor and allow for energizing relays upon which the activation of the mechanical components of the air conditioning system depends.

The full complement of micro switches is 11 for the temperature control system and 12 for the humidity control system. This difference is made up by the respective additions of Q607C and Q607D micro switches, both mounted at the opposite ends of the Step Controllers from the Modutrol motors.

Whilst both temperature and humidity control systems are very similar and sometimes may activate the same mechanical components,

they function quite independently. This may lead to paradoxical situations such as when heating and cooling occur simultaneously.

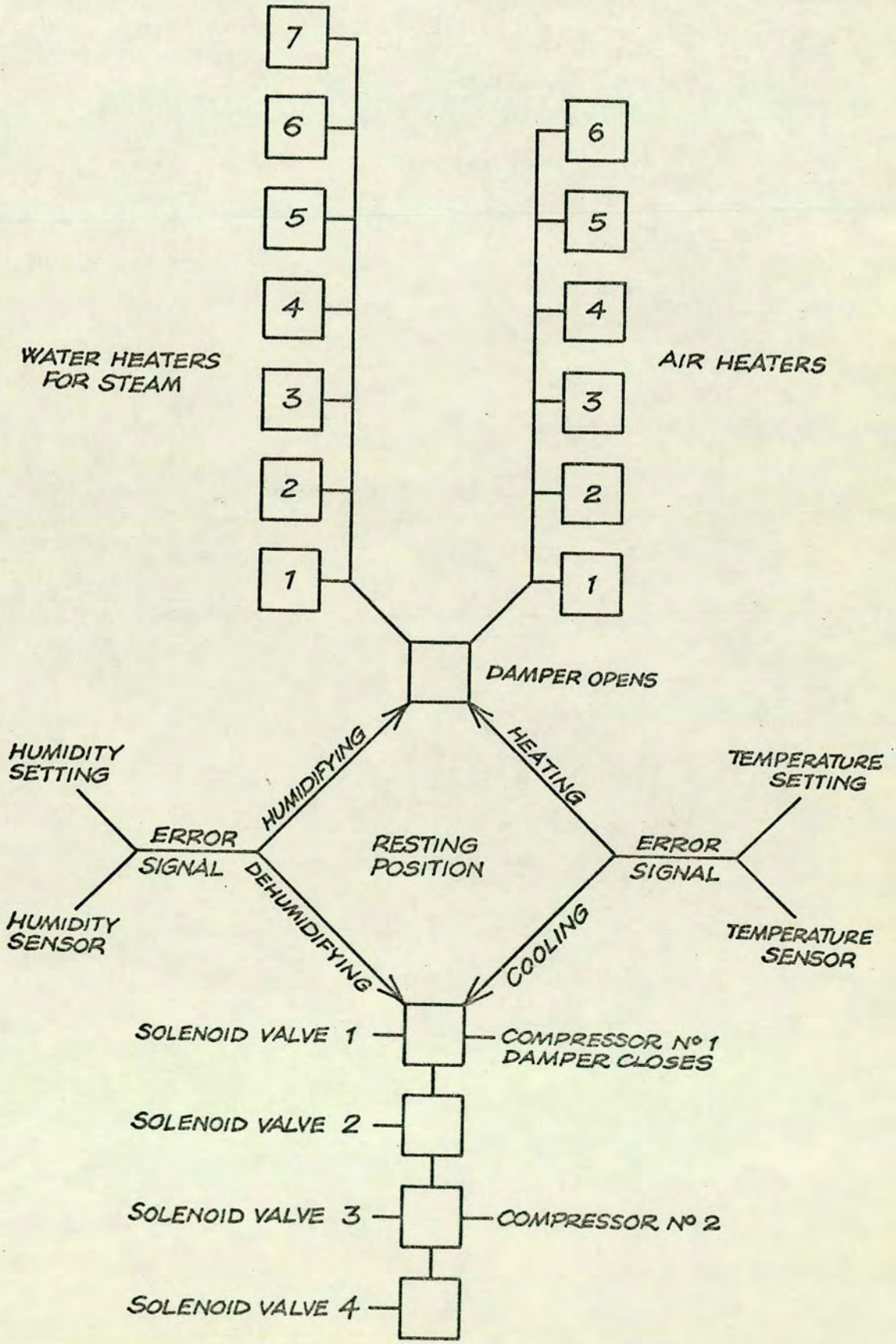
The scheme of operation of the various components is shown in Figure 6.22. To prevent overloading, the control system has to start from a 'resting' position before any of the elements may be activated. In situations where there is no demand for activating any of the air conditioning elements, the Modutrol motor assumes this position.

Air passing through the air conditioning unit is cooled by passing through a heat exchanger containing refrigerant. Whilst the maximum capacity of the cooling system is 9810 kg cal h^{-1}, the rate of cooling depends on the rate of air flow, the area of the radiator which is operational and the temperature of the coolant. The flow of air is regulated by a Modutrol motor operating a damper which when closed ensures that all the air passes through the heat exchanger. The effective area of the heat exchanger depends upon the action of the 2 compressors and, associated with them, 4 solenoid valves. The solenoid valves open to allow flow of liquid coolant to the expansion valves. The compressors and valves operate in sequence to raise the rate of cooling to a maximum; compressors 1 and 2 have powers of 1 kW and 1.5 kW respectively.

Heating occurs through the action of up to six 2 kW heating elements projecting into the air stream and operating sequentially. At the maximum rate of heating the total power consumption is 12 kW The damper is opened before any heating elements are activated so that air flow through the heat exchanger unit is restricted.

Humidity is reduced by condensation on the elements of the heat exchanger and is controlled in the same way as temperature reduction. Water is removed from the system by drainage.

FIGURE 6.22
SCHEMATIC DIAGRAM OF OPERATION
OF WIND TUNNEL AIR CONDITIONING SYSTEM



Humidity is increased by the production of steam from 4 water tanks in which seven 1 kW sequentially activated heating elements are submerged.

6.11 Operating experiences

During the execution of the long-term wind tunnel experiments, the functioning of the air conditioning system frequently created problems. These were partly due to the lack of maintenance contracts, which in the case of Jeffair Limited proved to be prohibitively expensive and the lack of qualified technical assistance within the Department.

Further difficulties were caused in earlier experiments by failure of equipment maintained by the Works Department upon which the pressure of the cooling water in the building depended. On occasions this would result in compressor failure and since, at that time, they were fitted with manual reset switches, temperature control could be lost unless frequently inspected. The safety of experiments has now been much increased by fitting automatic reset switches for the compressors, an alarm system to detect temperature deviations and an alternative mains water supply to the compressors in the event of failure of the cooling water supply in the building.

The Honeywell equipment, whilst providing excellent reliability in the temperature control system, functioned less effectively for humidity. During one experiment the automatic control system failed completely leaving the operator to adjust the controls manually over a considerable period.

The main fan operated without difficulty during all experiments but developed vibrations at high speeds which could be corrected

between experiments.

In view of the complexity of the wind tunnel installation and absence of previous development work, it might have been expected that experiments lasting several weeks at a time would be liable to interruption. On the whole, there were no major problems throughout the programme and no experiment had to be abandoned before its planned completion date.

SECTION 4.

EFFECTS OF WIND ON GROWTH AND YIELD

CHAPTER 7.

WIND AND PLANT GROWTH

7.1 Introduction

The results of the field experiments, although inconclusive, indicated that the growth of S.170 Festuca arundinacea was enhanced by shelter. Whilst in the sheltered positions other aspects of micro-climate may also have been altered, the reduction in wind speed was probably the most obvious direct effect. Thus, a more detailed study of the effects of wind on plant growth was considered to be an appropriate way of evaluating the role of shelter.

The effects of wind on plant growth have aroused interest over many years and have also stimulated various experimental studies. There seems to have been a generally held attitude, perhaps fostered by such obvious effects as the lodging of cereals and gross physical damage, that wind has an adverse effect on plant growth. This attitude extends into the earlier work as is apparent from a dissertation presented to the University of Bonn by Bernbeck (1907) entitled "Der Wind als pflanzenpathologischer Faktor". He also reported the considerable interest in wind in the last century in the following excerpt (Bernbeck 1924):

> "Die 'Windfrage' war im vorigen Jahrhundert heiss umstritten. Man konnte zu keinem befriedigenden Schlusse kommen, und noch vor etwa 20 Jahren war zwischen Hansen (Giessen) und Warming (Kopenhagen) eine grimme Fehde in Gange, ..."

"The wind question in the last century was hotly disputed. It was not possible to reach a satisfactory conclusion and so, for about twenty years, there was a fierce running feud between Hansen at Giessen and Warming at Copenhagen ...."

In the present century there have also been many attempts to assess the effects of wind on plants. Such attempts fall into two categories. Firstly there is a small number of experiments in which plants have been subjected to long-term wind exposures and the effects on selected aspects of growth examined. The experiments described in this section of the thesis fall into this category. Secondly there is a much larger number of experiments in which plants have been subjected to short-term wind exposures and any resulting physiological changes noted. The next section of the thesis examines some of the possible causes for the yield differences obtained in the wind tunnel experiments and reference is made to the literature on short-term exposures where appropriate.

7.2 Effects on growth

One of the early long-term experiments was carried out by Hill (1921). He used a fan "of the type used for ventilating war-ships" by means of which air could be drawn through a glass jar at a rate of 5m s^{-1}. Inside the jar, a damp cloth supported germinating seedlings of mustard or cress. The control was a similar jar without wind. He showed that wind considerably reduced germination and early development in both species and concluded "that the stunting effect produced by wind is not only due to a less favourable wetting, but to a greater

cooling. The growing point may be robbed by wind of heat which is produced in the cellular growth processes - heat which facilitates growth."

Bernbeck (1920) cited in Wadsworth (1960) also obtained greatly reduced growth in plants grown in the wind. In a reference to his thesis in 1908, Wrenger (1935/36) reported that he had found reductions in the development of stems and leaves of Helianthus annuus when exposed to wind.

Finnell (1928) at the Panhandle Agricultural Experiment Station in Oklahoma used marigolds as a test species to study the effect of physical damage by wind. He exposed 2 plants for 60 days to a 6.7m s^{-1} wind produced by a 30 cm electric fan. Two plants in comparatively still air acted as controls and the whole experiment was carried out in a greenhouse. Water supply was maintained at a high level by daily watering. Although very limited in scope, his results showed that in the plants exposed to wind, some of the foliage was destroyed by wind whipping. Also, the rate of growth as measured by increments in plant height was reduced initially but later increased as the plants extended above the range of the fan. After 60 days, the final dry matter yields were reduced by 49% but the number of secondary branches was increased by 43%, although these results were probably not statistically significant.

Further work by Finnell (1929) showed that when sorghum and barley were grown for 40 days in a wind of about 6.7m s^{-1}, growth was reduced by 30% and 24% respectively compared to that in the unexposed control plants. His data suggested an early divergence and later convergence of growth especially in sorghum grown in clay pots. In this case, growth was actually higher in the wind exposed plants for the last 20

days of the experiment thus reversing the earlier trend. He concluded that wind did considerable damage to plants even when supplied with additional water to meet the demands of increased water loss.

Martin and Clements (1935) carried out the most comprehensive of the earlier studies using Helianthus annuus. They selected a "natural wind" as a control and 3 test wind speeds of 2.2, 4.5 and 6.7 m s^{-1} produced by 51-56 cm fans. Each treatment was applied to a set of 6 plants. The experiments lasted between 42 and 59 days and were repeated 4 times, the whole series being carried out over a 2-year period. In each experiment, the leaf area, stem height and diameter, and dry weight all decreased with increased wind velocity. The 6.7m s^{-1} treatment caused reductions in dry weight of between 33% and 50%.

Wrenger(1935/36)carried out a series of 200 experiments on 38 species of plants! The main interest was in the effect of wind on transpiration but some data on growth were also obtained. Plants of H. annuus were exposed to a wind of 1.5m s^{-1} for 5 weeks with similar plants in still air acting as controls. She found no effect on plant height but leaf area was affected by wind. The total leaf area of 24 plants was 664.2 cm^2 for wind exposed plants and 756.4 cm^2 for the controls. She noted that not only did the control plants have larger leaves but also a faster rate of development of new leaves.

Rao (1938) carried out an investigation on the Italian millet, Setaria italica using one wind speed,mostly 4.9m s^{-1}, and a control. Again,a fan was used for generating the wind. The wind exposed plants grew more rapidly than the controls during the first 13 days but less rapidly thereafter. The tops of the exposed plants were shorter, lighter in weight, thinner stalked and had narrower leaves and fewer tillers. These plants also had less well-developed root systems. If

his data for plant height are examined in detail, it appears unlikely that the differences between the two treatments were statistically significant except perhaps towards the end of the experiment. Rao suggested that the initially more rapid growth of the wind exposed plants might have been due to a cooling effect of wind during a period of very high temperatures.

The first long-term experiment on trees was carried out by Satoo (1948a) in which he examined the effect of wind on the growth of seedlings of Robinia pseudacacia. He used 2 soil moisture regimes, one set at 80% of saturation and the other at 40% of saturation. The experiment was carried out in a greenhouse at a mean air temperature of 27°C. The wind speeds used were 3.7m s^{-1} and 3.5m s^{-1} with one fan for each wind treatment, the fans being alternated between the 2 soil moisture treatments. The experiment lasted for 4 weeks and was terminated by a destructive harvest. He found that the number of leaflets, number of leaves, number of leaflets per leaf, height, stem diameter at the base and the dry weight of the tops were all reduced by exposure to wind. Where soil moisture was adequate, the effects of wind was significant only for dry weight and height reductions; where soil moisture was deficient, the effects were much greater and were significant for all parameters. Satoo (1955a) also showed a similar effect with Quercus acutissima.

These results are in general agreement with those of previous experiments where water supply was not limiting but the additional evidence of an interaction between the availability of soil moisture and the response to wind exposure is especially interesting. This would corroborate the observations that shelter is more effective in the drier areas of the World (Marshall, 1967).

Apart from the work by Hill, the other yield experiments have all used fans blowing directly on to the plants as a means of producing a wind exposure. By using a wind tunnel, far more accurate control of wind speed is possible and, depending on the sophistication of the design, spatial and temporal variations can be much reduced and wind profiles developed. The idea of using wind tunnels with plants is by no means new; Blackman and Knight (1917) devised an 'air-flue' in which they were able to look at transpiration losses from plants with minimal variation in temperature and relative humidity.

The first long-term experiments using wind tunnels were carried out by Whitehead. One of his main interests was in the adaptive responses of plants grown in windy conditions. Whilst for the purposes of this section of the thesis only his yield results are of concern, his papers also contain much information on anatomical and morphological adaptations. His original ideas stemmed from observing the much reduced forms of plants growing in exposed areas such as Monte Maiella in Italy. (Whitehead 1954). He found that reducing the wind by erecting low stone walls caused an increase in height of the enclosed vegetation. He considered that this reflected the phenotypic plasticity of the plants, a feature having adaptive value. This term has been defined by Bradshaw (1965) as being shown by a genotype when its expression is able to be altered by environmental influences. Any changes so manifested may be physiological or morphological.

Whitehead (1957) examined the effect of 4 wind speeds on the height and dry matter production of Cerastium atrovirens, Hordeum vulgare, and Senecio nebrodensis. Each species was respectively classified as being exposure evading, exposure tolerant, and exposure sensitive. The wind speeds used were 0.11, 4.0, 11.2 and 26.8m s^{-1}. C.atrovirens was hardly

affected by wind both in terms of dry weight or height. H.vulgare showed little reduction in dry weight but a greater reduction in height. S. nebrodensis showed a marked reduction in both height and especially dry weight which was reduced almost to zero at the highest wind speed. This species thus showed the greatest degree of phenotypic plasticity. Whether a low wind speed of 0.11m s^{-1} is realistic in view of the circulation necessary to ensure accurate temperature control or whether a high wind speed of 26.8m s^{-1} at crop height in Britain is realistic is perhaps questionable.

Whitehead and Luti (1962) compared the growth of 2 varieties of Zea mays with no wind and with a 14.8m s^{-1} wind in a wind tunnel for 40 days. The plants were grown under artificial light with an intensity of 5160 lux. Nodak 301, grown without wind, had a mean dry weight per plant of 0.85 g but, in a wind of 14.8m s^{-1}, this was reduced to 0.49 g. Southern Sweet Corn had dry weights of 0.42 and 0.28 g respectively. The root:shoot ratio increased from 1.07 to 1.23 in Nodak 301 and from 1.80 to 2.11 in Southern Sweet Corn.

The light intensity in this experiment was very low and equivalent to a deep shade. It is therefore possible that the responses to wind might have been more exaggerated than normal due to the plants being etiolated.

In a further study on Helianthus annuus, (Whitehead, 1962), wind speeds of 0.45, 4.0, 8.5 and 14.8m s^{-1} were used. The light intensity was again 5160 lux with a 14-hour day and a 10-hour night. After 30 days, the experiment was terminated by a destructive harvest. There were substantial reductions in total dry weight, shoot dry weight, internode length and leaf area with increasing windspeed. Root dry weight was slightly reduced, thus the root:shoot ratio rose with

increasing windspeed. The dry weight increment per unit area of leaf per unit time remained very constant at all windspeeds, so it was concluded that wind affected the mechanism in the plant which determines or controls leaf expansion.

Whitehead considered that the reductions in growth were in part due to a water stress, resulting from exposure to wind. To support his hypothesis he grew Helianthus annuus at various levels of soil moisture down to 0.031 of field capacity (Whitehead, 1963a). He found similar results to the previous experiment, but with the exception that the dry weight accumulated per unit leaf area fell markedly at soil moisture levels less than 0.125 of field capacity.

This approach was critised by Humphries and Roberts (1965) who pointed out the difficulty of artificially maintaining an even distribution of soil water in soils at much less than field capacity. Whitehead (1965) explained that water was added to the pots by means of a syringe so that small amounts could be introduced into the soil at different depths.

Pursuing the idea of adaptation to wind, Whitehead (1964/65) then exposed plants of H. annuus previously subjected to windspeeds of 0.45, 4.0, 8.5 and 14.8m s^{-1} to a windspeed of 17.9m s^{-1} and recorded the time taken for "death" to occur. He found that the plants grown originally at 0.45m s^{-1} died after 0.5h, those at 4.0m s^{-1} after 1h, those at 8.5m s^{-1} after 3h and those at 14.8m s^{-1} were still living after 6h of exposure. A similar trend was noted in plants which had been exposed to varying degrees of drought before being subjected to a 17.9m s^{-1} wind. This work was intended to illustrate that plants once adapted to wind or drought are then better able to withstand extreme winds. It is questionable whether a 17.9m s^{-1} wind at plant height is very reali-

stic and also whether the very short times required to produce "death", although differing with treatments, have much meaning. From his other experiments, it would seem that the plants which previously had been exposed to higher levels of wind or greater degrees of drought would have been much smaller. Thus, in addition to the morphological changes shown previously, the comparison of survival at 17.9m s^{-1} was also one between plants of different sizes.

Whitehead (1963b) noted that plant anatomy and morphology were also affected by plant growth substances. Using Helianthus annuus var. Pole Star, he then compared the effect of an application of β indole acetic acid using wind speeds of 0.45, 4.0, 8.5 and 14.8m s^{-1}. The untreated plants used as controls showed similar responses to wind exposure in relation to leaf area, average internode length, shoot dry weight, root dry weight and root:shoot ratio as reported by Whitehead (1962). There was no significant effect of I.A.A. on any of these parameters.

A second experiment applying 1% gibberellic acid, this time with windspeeds of 0.45, 8.5 and 11.2m s^{-1}, again showed a similar trend for the untreated control plants. However, those plants treated with G.A. showed far less reduction of leaf area, internode length, shoot dry weight, root dry weight and little change in the root:shoot ratio. An application of 1% G.A. to plants grown under different degrees of drought similarly showed less reduction in internode length and leaf area compared with the control plants. Whitehead considered that G.A. had induced a reduction in phenotypic plasticity and therefore a loss of ability to withstand extreme exposures. This he tested by exposing plants, previously grown in differing degrees of drought and then sprayed with 1% G.A., to a 17.9m s^{-1} wind and noting the time to "death". All the plants treated with G.A. were killed after about 1 hour, whilst the control plants grown

at 0.125 of field capacity lasted up to 5 hours.

Whitehead (1964/65) then argued that, since gibberellins had reduced the ability of Helianthus annuus to survive extreme exposures, the application of anti-gibberellins should have the opposite effect. In this paper, he reported an initial trial with (2-chlorethyl) trimethylammonium chloride in which plants so treated appeared undamaged after several days exposure to a wind of 17.9m s^{-1} despite being initially grown in mesophytic conditions. However, he later reported (Whitehead, 1968) that further work on this approach had proved inconclusive.

These interesting experiments tend to be difficult to evaluate because of the lack of detailed information about the experimental conditions and the variability of the results.

Warren Wilson (1959) was also interested in the relationship between wind and the survival of vegetation especially under arctic-alpine conditions. In one experiment, he artificially erected a branch of Salix arctica and compared the effects of the extra exposure on the growth throughout a season. He found that bud mortality increased and leaf size and shoot elongation decreased compared to normal prostrate branches. He also examined the net assimilation rates of detached leaves of Oxyria digyna and found a rate of 34g. m^{-2} $week^{-1}$ from a wind swept summit and 46g. m^{-2} $week^{-1}$ from a sheltered hollow. His most interesting experiment was with Brassica rapa where he grew seeds in pots containing unmanured soils and exceptionally fertile soils from beneath birdcliffs. When the cotyledons were partly expanded, the pots were then placed either on a windswept summit or a sheltered hollow, each pot being sunk level with the ground surface. After 38 days, when 2-4 leaves had been formed, the plants were harvested. His data on relative growth rates expressed as g g^{-1} $week^{-1}$ are shown below:

	Normal soil	Manured soil
Windswept summit	0.06	0.29
Sheltered hollow	0.10	0.39

The differences in growth rate due to exposure were not as great as those due to variation in soil fertility. The suggestion of an interaction between nutrient levels and exposure is especially interesting in view of the field experiments at Liberton.

In contrast to the wind tunnels used by Whitehead which had working sections in parallel, Wadsworth (1959) carried out a series of experiments at Reading using a wind tunnel with working sections in series. The cross-sectional area of each of the 4 sections was half that of the previous one; the narrowest section was 21.5 cm in diameter and the widest was 61 cm in diameter. Each working section had parallel sides and was joined to the next section by a contraction cone of 21^{o} total angle. Air was drawn by a 30.5 cm diameter airfoil fan from the largest to the smallest section. The windspeeds produced were equivalent to about 1.2, 2.7, 5.8 and 12.0m s^{-1} at a height of 1m. Other than windspeed, there was no further control of climatic variables.

Rather than concentrating on production, Wadsworth used growth rates as a basis for comparing the effects of different wind treatments. In one experiment (Wadsworth, 1959) he compared the growth of B. napus in the 4 sections of the wind tunnel using plants of 3 different sizes. When the plants were less than 1 cm tall, the relative growth rates increased with increasing windspeed. Plants 1-4 cm tall had the highest relative growth rates in the section with a windspeed of 2.7m s^{-1}, but lower rates at the higher windspeeds, thus suggesting an optimum windspeed for plant growth. The largest plants, which were 4-7 cm tall, showed a decrease in relative growth rates as windspeeds increased.

Measured at plant height, the optimum windspeed was about 0.3m s^{-1}. The idea of an optimum windspeed is certainly interesting but, if of general occurrence, the specific values will be dependent upon the size of the plant, the species, and other environmental factors. Wadsworth (1964) was careful to stress this point. In fact, he used extremely small plants and it is open to question whether his smallest plants, in particular, protruded above the boundary layer associated with the floor of the tunnel. It would have been useful to have had more accurate figures about the windspeed in the crop.

In a further series of experiments, Wadsworth (1960) compared the effect of wind on B. napus, Hordeum vulgare and Pisum sativum when grown in water culture. For this work, he was able to measure windspeeds more accurately and noted that a boundary layer was formed rapidly after each contraction. Decreases of windspeed near the tunnel floor were found in the first 3 cm in the 2 widest sections, the first 2 cm in the third widest section and the first 1.5 cm in the narrowest section. Thus in his previous experiments the smallest plants would have been growing well inside the boundary layer at all windspeeds.

In the water culture experiments, the windspeeds amongst the plants were approximately 0.3, 0.7, 1.7 and 4.0m s^{-1}. His results showed no significant variation in relative growth rates or net assimilation rates with any of the 3 species. This would suggest that when water supply is non-limiting the effects of wind on plant growth are likely to be much reduced. In several of the other experiments described in this chapter, attempts were made to maintain a non-limiting water supply. Nevertheless, the actual availability to the plant is likely to have been restricted compared with water culture because of the limitations imposed by the movement of water within the soil.

Winter (1964/65) was also interested in the effect of wind on plants in relation to water supply. This interest arose from the need to assess the relative merits of shelter and irrigation in increasing the yields of certain vegetable crops. The wind tunnels used were relatively unsophisticated in design producing windspeeds of 2.44m s^{-1} and, by means of an enclosure within the "working section", a control of no wind. During the experiments, the temperature was maintained at 24°C, the relative humidity at 60% and the light intensity at about 3440 lux at plant height. Apparently the control plants were grown in conditions which, other than wind velocity, were not materially different. Potatoes, when exposed to wind, showed lower rates of growth as measured by crop height than the controls. In this situation, the wind was only switched on during the 12-hour day. In other experiments with peas and potatoes, the effect of wind during the day was much greater than wind during the night. Water culture experiments with tomatoes showed that the loss of water from the wind exposed plants was considerably less than from the controls. This was considered to be due to stomatal closure, a hypothesis confirmed by infiltration studies with ethylene glycol - butyl alcohol. Winter suggested that stomatal closure, due to wind-induced water stress during the day, also interfered with gas exchange and so reduced yields. Thus he concluded that irrigation was not likely to obviate the adverse effects of wind on crop yields.

Further long-term studies on the effects of wind on growth were carried out by Tsuboi (1961) with rice. He used two wind tunnels, a large modified Eifel type operating outside and a smaller closed-circuit type housed in a building. The smaller tunnel (also having control over temperature and humidity) was similar to that used for the experimental work in this thesis.

He found that over a range of velocities from 3-12m s^{-1}, the yield of rice decreased exponentially with wind duration and in proportion to the 3/2 power of wind velocity. The degree of damage was found to increase with decreasing humidity, decreasing soil moisture, by cutting some of the roots and also at lower root temperatures. He observed that there was desiccation of the tips of the leaves in wind and that this was a characteristic feature of wind exposure rather than drought exposure. In particular, there was an effect resulting from the motion of the leaves in the wind. By controlling the motion of the plants when exposed to strong winds, he found that 10-25% of the reduction in yield was alleviated and that the injury to leaves and ears was small.

Thus this experiment draws attention to possible differences between laminar and turbulent flow in relation to plant growth. There is no information in the literature reviewed in this chapter about the levels of turbulence experienced by the plants which can be interpreted in aerodynamic terms. This would certainly be of interest. Wadsworth (1960) states that smoke tests in his wind tunnel revealed little turbulence and this would be expected because of the contraction and a mesh screen between each of the working sections.

7.3 Effects on anatomy

In addition to yield differences, wind has also been shown to cause less obvious effects on growth such as changes in anatomy. Martin and Clements (1935) for example, also carried out anatomical investigations on Helianthus annuus. In microscopic examinations of the mesophyll, they were unable to show any marked differences, but the xylem in the stems showed changes in proportions of the various elements and a decrease in area. This decrease in area was matched by similar responses for the stem as a whole so the proportion of xylem did not change.

Some of the work by Whitehead emphasized the anatomical changes accompanying the morphological manifestations of phenotypic plasticity. In Zea mays, Whitehead and Luti (1962) found that leaves exposed to a 14.8m s^{-1} wind were wider and thicker and the sclerenchymatous margin was 6 times as wide as the controls. The degree of vascularization was greater; there were many more large vessels in the treated plants, the phloem elements were almost twice as long and there were almost 3 times as many fibres per bundle.

Venning (1948) examined the formation of collenchyma in celery petioles in 2 sets of plants grown in a greenhouse, 1 set being subjected to wind produced by a fan. The plants exposed to wind motion were found to differentiate the same number of collenchyma bundles but,within the bundles,there were larger areas of collenchyma, heavier thickenings of the cell wall and the collenchyma cells also had larger diameters.

7.4 Conclusions

This review has shown that, except at low velocities, wind is likely to reduce plant growth and may also cause anatomical changes. Any reduction in growth is likely to be increased by increasing velocity and turbulence and by decreasing water supply and humidity. It seems likely that these effects may also be influenced by the nutrient status of the soil. Of all the experiments reported, no work has been carried out on a herbage species although the experiments with rice, barley and Italian millet are certainly relevant. Thus, apart from the need to examine the effect of wind on F. arundinacea in relation to the shelter experiments, there was also a clear need to investigate how wind affects the growth of grass in general.

CHAPTER 8.

WIND TUNNEL YIELD EXPERIMENTS - GENERAL APPROACHES

8.1 Introduction

The major effort of this thesis consists of a series of wind tunnel experiments designed to examine the effects of wind on the growth of S.170 Festuca arundinacea. In the field situation, wind of course does not act independently of other factors in determining yield, rather the situation is complex and many interactions may be expected. To explore fully many of these wind effects would have been well beyond the scope of this thesis; instead, the experiments covered certain limited aspects selected with regard to the field experiments. As explained in Chapter 5, the field experiments sacrificed replication for comprehensiveness and, by so doing, lost precision. In the wind tunnel experiments, a simpler design was used asking fewer questions but with greater precision. Two main questions were asked:

1. What is the effect of wind on the growth and yield of S.170 F. arundinacea ?
2. Is any effect influenced by the levels of available nitrogen and phosphorous ?

It was decided that these questions could be most effectively answered by the use of a factorial design incorporating 2 levels of wind (W_1 and W_2, 2 levels of phosphorous, (P_1 and P_2), 2 levels of nitrogen, (N_1 and N_2) and 5 replicates).

This chapter is concerned with the aspects that were common to all the wind tunnel yield experiments. The individual details of the experimental preparation, plant culture, final harvest procedure and the results are described in the chapter appropriate to each experiment.

8.2 Experimental conditions

One of the first questions considered in this series of experiments was how to decide the levels of the various factors involved. In keeping with the original aims of the investigation, conditions were chosen that would realistically reflect those likely to be experienced by plants in eastern Scotland in spring. Some guidance in this was available from the measurements of air temperature, soil temperature and run of wind taken during the field experiments which were described in section 2. An additional problem was the selection of values for the 3 experimental variables which, in addition to being realistic, would also contrast sufficiently to produce effects on plants.

For all experiments, the air temperature in the wind tunnel was set at $5.5^{o} \pm 0.5^{o}C$, a temperature at which growth, albeit slow, could certainly be expected. Reference to the mean temperature values in Table 3.4 shows that this was quite realistic of the early part of the growing season.

No data was available on relative humidity from the field experiments and so this was fixed at $80 \pm 2\%$, a generally realistic level confirmed by Meteorological Office Climatological Memorandum No.35 (1962).

The literature review in Chapter 7 indicated that reduced availability of soil moisture was likely to increase the effect of wind exposure. In spring in eastern Scotland,it was considered that soil moisture would be non-limiting and this situation was simulated in the wind tunnel experiments by watering at the first sign of surface dryness of the peat. Whether this was realistic of field conditions in recent years,when there have been a succession of dry springs,is perhaps questionable. If this trend continues, future experiments might very usefully introduce soil moisture as a factor.

Ideally, a controlled environment wind tunnel should allow for the simultaneous comparison of the effects of several windspeeds on plant growth under otherwise identical conditions. In the tunnels used by Whitehead, this was attempted by dividing the working section into four parallel compartments at the front of which the air flow could be controlled. The difficulty with this approach is the size of the installation necessary if problems due to the growth of the boundary layer on the walls are to be avoided and if a realistic profile is required. It was considered that such an approach was not desirable and therefore alternatives were examined.

One alternative would have been a series of experiments, each at a single windspeed, running consecutively. It would have been essential to ensure that exactly the same conditions were used in each experiment and it was considered that this would have been a practical impossibility.

The method finally adopted, which proved to be extremely arduous, was a system of regular alternation of 2 windspeeds within the tunnel every 12 hours. By synchronously changing over 2 sets of plants, it was so arranged that each set was exposed to a 12-hour day in the wind tunnel and to a 12 hour night in a controlled temperature room elsewhere in the building. Thus, each set of plants, apart from being 12 hours of of phase was, other than the wind treatment, subject to exactly the same conditions.

In deciding on the two windspeeds, the data from the field experimentswere particularly useful. The average speeds at Liberton are shown in Table 3.4 and ranged from 3.16m s^{-1}, the highest value in the exposed position, to 0.29m s^{-1}, the minimum value in the north facing position. In the Lammermuirs' experiment (Table 4.1),windspeeds ranged from 6.74m s^{-1}, the highest value in the position north of the shelterbelt, to 1.44m s^{-1}, recorded from one of the anemometers within the shelterbelt.

The higher windspeed was fixed at the realistic value of 3.5m s^{-1}. In considering the lower windspeed, the idea was to have a minimal circulation rather than no wind at all which would obviously have been unrealistic. The lowest speed possible in the working section was 0.6m s^{-1} and this seemed a reasonable value to adopt.

As both sets of plants only experienced a wind exposure for 12 hours each day, the averages over 24 hours would have been 0.3m s^{-1} and 1.75m s^{-1}, but these figures are uncertain since they entirely discount any air movement in the dark period. To ensure adequate temperature control, the rooms used for the dark period obviously had some air circulation. In the field, wind does not exclusively occur in the day, nevertheless, because of reduced turbulence, the average windspeeds at night tend to be lower.

In subsequent discussion about wind, the 0.6m s^{-1} treatment will be referred to as W_1 and the 3.5m s^{-1} treatment as W_2. These values were averages of measurements of windspeed made at 9 positions across the floor of the working section. A vane anemometer (Airflow Developments Ltd.) supported at crop height on a board covering the entire floor was used for this purpose.

Sweeney (1969) has described the circadian rhythms of many plants and has shown that a rhythm, once established, may persist for several days after plants are moved to a new environment. This aspect was taken into account in the preparatory period in the growth chamber before starting an experiment in the wind tunnel. In the growth chamber the lights were adjusted to give a 12-hour day but phased from 06.00 to 18.00. The W_1 and W_2 groups of plants were changed over every 12 hours at 12.00 and 24.00 so that each treatment would initially be 6 hours out of phase with the previous conditions in the growth chamber. The phasing of the treatments in each experiment was as follows:

0.00h to 12.00h	W_2 plants in wind tunnel; lights on.
	W_1 plants in growth room; lights off.
12.00h to 24.00h	W_1 plants in wind tunnel; lights on.
	W_2 plants in growth room; lights off.

One danger of such an approach was that the effects of the wind treatments might have been confounded with effects due to the diurnal fluctuation of other environmental factors, especially carbon dioxide. The selection of 12.00 and 24.00 as times for changing over the boxes was fortunate in this respect. As an extra precaution, the carbon dioxide concentrations were monitored over several 24-hour periods; the details of this are described in Chapter 14. In the W_2 treatments, prior to the start of each experiment, the speed of the main fan was adjusted so that measurements taken at the same 9 positions averaged 3.5m s^{-1}. To ensure that conditions remained constant during experiments, the speed control on the main fan was locked and the regular alternation of the two windspeeds was achieved by switching the main fan on and off. There was no means of varying the windspeed in the W_1 treatment as this was produced by the action of the centrifugal fan alone.

In the presence of a crop, the windspeeds would be expected to be modified by the development of a profile. The speed at crop height was measured with a vane anemometer on 29.3.1971 towards the end of yield experiment 1. Each of the 20 positions used for the hot-wire measurements were also used for this purpose. Readings were obtained by removing a box and substituting the anemometer so that the centre of the anemometer head was level with the average height of the crop; i.e. 15 cm. As the head was 10 cm in diameter, the readings obtained were an integration over a relatively large area.

The values for the 20 positions in the W_1 and W_2 treatments are shown in Figures 8.1 and 8.2 respectively. When the values in each treatment were averaged, the corresponding windspeeds were 0.62m s^{-1} and 3.80m s^{-1}. In Figure 8.2, the tendency for the velocity to fall associated with profile development can be clearly seen and this is also true of Figure 8.1, although, because of the lower values, this is rather less obvious.

No such measurements were taken in the other yield experiments, since, with care taken to ensure that the W_2 velocity averaged over the 9 positions was the same in each, it was assumed that there would also be similar speeds at crop height when measured in the full 20 positions.

The nutrient levels used for the wind tunnel experiments were also based on the experience gained in the field experiments, but with certain modifications to ensure greater precision. The difficulty with hoof and horn as a source of nitrogen and superphosphate as a source of phosphorus was to know how much of the two elements would be available to the plants. Both sources were variable and of low solubility. The use of hoof and horn was therefore discontinued and the source of phosphorus changed to soluble di-sodium hydrogen orthophosphate dodecahydrate.

Another problem was the possibility that urea, which was added as a soluble source of extra nitrogen, could produce phytotoxicity. Stephen and Waid (1963) have reported toxicity in a variety of crops where urea was applied at high levels, effects not noticed with similar high applications of ammonium nitrate and ammonium sulphate. Devine and Holmes (1963) have reported higher yields from grassland treated with ammonium nitrate and ammonium sulphate than with the same quantities of urea. Court, Stephen and Waid (1964a and 1964b) suggested that part of the toxicity of urea is associated with the accumulation of quantities of ammonia and nitrite. This was also found by Barrett (1968) in his

FIGURE 8,1
WIND TUNNEL YIELD EXPERIMENT 1
W_1 CONDITIONS
WIND VELOCITY AT CROP HEIGHT MEASURED AT 20 POSITIONS

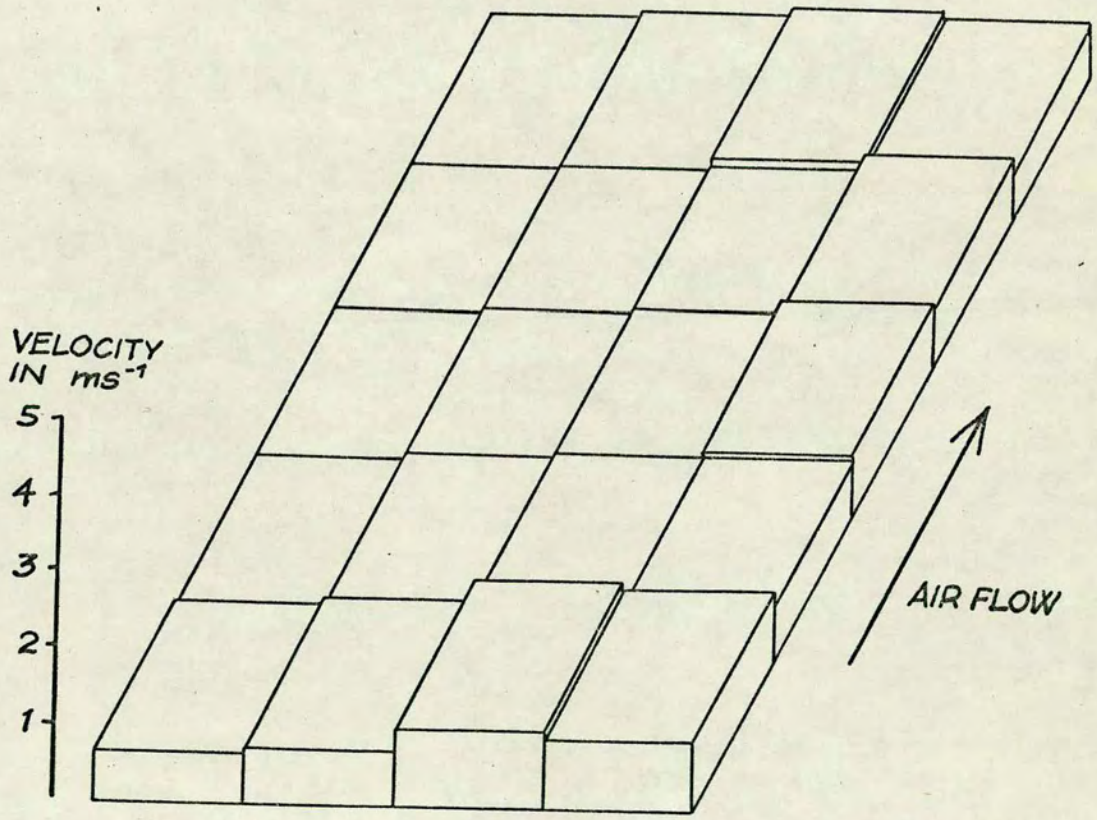
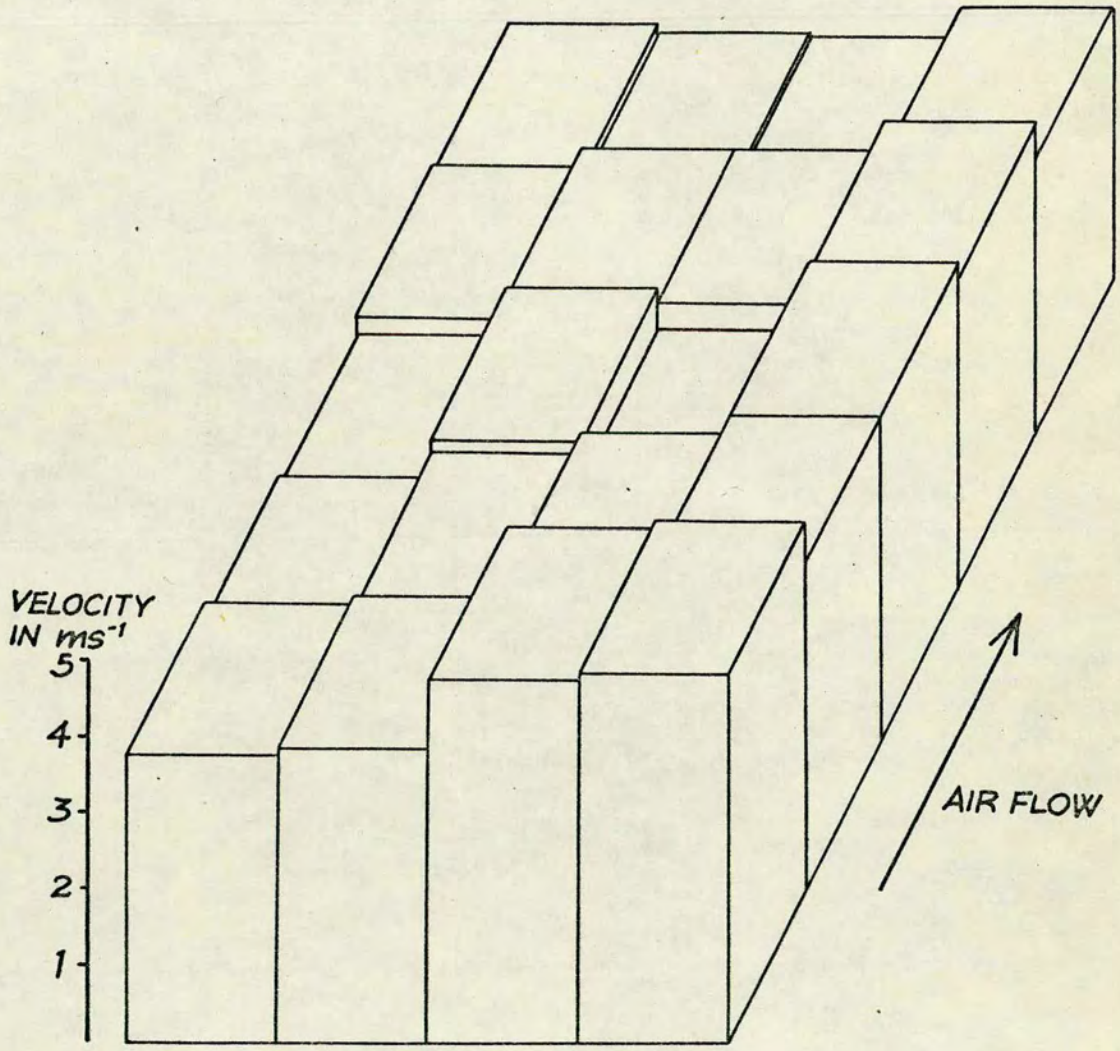


FIGURE 8,2
WIND TUNNEL YIELD EXPERIMENT 1
W_2 CONDITIONS
WIND VELOCITY AT CROP HEIGHT MEASURED AT 20 POSITIONS



experiments with peat and sand mixes but only at low light intensities. Because the wind tunnel experiments were conducted at fairly low light intensities (60.2W m^{-2}), it was decided to change the source of soluble nitrogen to ammonium nitrate. The 25 g. of urea which were added to the high nitrogen treatments in the field experiment were equivalent to about 600 parts per million. As there was certainly no evidence of deficiency at this level, the same quantity was used for the high nitrogen application of ammonium nitrate in the wind tunnel experiments.

Both di-sodium hydrogen orthophosphate and ammonium nitrate have the advantage that they can be varied without any expected effects on other nutritionally important elements. The final levels of both nutrients selected were 10 p.p.m. (P_1) and 45 p.p.m. (P_2) for phosphorus and 21 p.p.m. (N_1) and 621 p.p.m. (N_2) for nitrogen.

Certain other modifications to the U.C. mixes (Matkin and Chandler, 1957) were made for the wind tunnel experiments. Work by Barrett (1968) on the evaluation of various rooting media showed that the fresh weight production of container grown plants was directly proportional to the water holding capacity of the rooting medium used. In peat and sand mixtures this is proportional to the amount of peat. Barrett concluded that a mixture of 75% Sphagnum peat: 25% fine sand was the most suitable mixture and so this was used throughout the wind tunnel experiments.

In the field experiments, Tay gravel had been used as the nearest approximation to fine sand. In the wind tunnel experiments this was replaced by a very pure fine sand corresponding much more closely to the specifications of the U.C. mixes. As before, the peat used was a high grade Sphagnum type.

8.3 Experimental procedure

The growth medium was thoroughly mixed and nutrients added in a similar manner as in the field experiments. As no source of phosphorus would otherwise have been available for the plants, soluble phosphorus was added during the initial mixing at between 5 and 15 p.p.m. The levels were eventually raised towards the start of the period in the wind tunnel. Nitrogen was added in the same way as in the field experiments as potassium nitrate at a rate of 21 p.p.m. but hoof and horn was intended to be excluded from the mixture. During the mixing, the following fertilizers were added per 1000ℓ of peat and sand:

Potassium nitrate	148 g	
Potassium sulphate	148 g	
Dolomite lime	4446 g	
Calcium carbonate lime	1480 g	
Di-sodium hydrogen orthophosphate	58 g	(P_1)
Di-sodium hydrogen orthophosphate	173 g	(P_2)

In these experiments, a different set of boxes measuring 28 cm x 20 cm x 15 cm deep were used. These were designed so that a 4 x 5 block arrangement would fully occupy the floor of the working section of the wind tunnel. Constructed from 18-gauge galvanized iron sheeting, they were then coated internally and externally with 3 layers of polyurethane varnish to obviate any problems with zinc toxicity. The internal volume of each box was 8.15ℓ and this was filled with 10ℓ of uncompressed mix. After filling, the boxes were watered heavily and allowed to stand.

The growth of young plants is usually exponential (Blackman, 1960) and therefore the final yield is dependent both on the initial size of the plant and its subsequent growth rate. Because of this, careful

attention was paid to plant culture and randomization in the early stages of growth to ensure that variation in the initial size of the plants was minimised. There were two main sources of such variation in the experimental system, that between boxes and that between individual plants. Only the first source was of concern since the results were evaluated on the basis of means of the 8 or sometimes 4 experimental plants per box.

In each experiment, the early stages of growth took place in a greenhouse and later, the plants were transferred to a growth room to adapt them to the experimental conditions of the wind tunnel.

The seeds were first germinated in shallow trays containing a 75% peat: 25% sand mixture with no added nutrients. When the second leaf was about to emerge, which was usually about 2 weeks after sowing, the seedlings were transplanted to the experimental boxes. It was found that transplanting at this stage,when the plants were about 5 cm tall,was usually totally successful and any failures were always under 1%. Within the boxes,the seedlings were arranged by means of a grid into a 5 cm square spacing giving 24 plants per box in 4 rows of 6 plants. The same criteria in selecting plants for transplanting were used as in the field experiments.

After transplanting, the plants were watered heavily and then allowed to grow in the greenhouse before transferring to a growth chamber maintained at $10^{o}C$. After one week, the temperature was lowered to about $5^{o}C$, the operational temperature of the wind tunnel. During this period of adaptation, the plants were clipped to 8 cm to simulate a light grazing and nutrients added as appropriate, so that by the time the plants were placed in the wind tunnel, all nutrient treatments had already been imposed.

The wind tunnel experiments usually lasted about 55 days and, for

experiments of this type, required an unusually large amount of routine maintenance. Not only was this required to ensure the smooth operation of the wind tunnel, but also for the regular changing over of the treatments. During this process, care was taken to minimise the transit time between growth chamber and wind tunnel. Within a 24-hour period, the boxes were not normally exposed to ambient air temperatures for periods longer than 20 minutes for this purpose.

To minimize the effects on yield of the velocity gradient along the length of the working section, the positions of the boxes were randomized every 24 hours during a changeover. The positions within the replicates were randomized once every week, but no attempt was made to maintain these positions.

During the 4 yield experiments, little attempt was made to measure physiological or physical parameters which might have explained some of the yield differences obtained. Whilst this would have had value, some disturbance of the experimental conditions would have been inevitable. It was considered that such measurements should be restricted to situations where any resulting yield effects would be of no consequence.

8.4 Weekly tiller counts

Prior to the start of the wind tunnel experiments, the tillers in the central 8 plants of each box were counted and, thereafter, the same plants were counted each week for the duration of the experiments. This precluded the difficulty experienced in the field experiments with the selection of 5 out of a possible 8 plants for counting. The same criteria for counting tillers were used as in the field experiments, tillers less than 2 cm in length being excluded.

8.5 Final harvest procedure

In all experiments, the harvest procedure was similar to that in the field experiments, but was much more detailed. A particular effort was made to examine root production. Whitehead (1962) showed that the root:shoot ratio was increased by exposure to wind - so it was therefore of interest to know whether this effect would also occur in F. arundinacea.

Initially, the outer 16 plants were clipped below the soil surface and any adhering soil particles and roots removed. These plants were dried in a forced-air drying oven at 80°C and then ground and stored for later nitrogen and phosphorus analyses.

The central 8 plants in each box were separated out as entire plants by washing the soil from the boxes and teasing out the roots. The density of roots was quite high so that separation was not easy and it is quite likely that certain roots were broken and lost, although the proportion was probably quite small. This method would certainly be unacceptable if absolute values of root growth were the main object of the experiment, but it was still considered worthwhile for comparative measurements between treatments. After separating the plants, the roots were carefully washed to remove any adhering peat and especially sand particles before being clipped off and dried. The aerial parts were then separated into live leaves, dead leaves and the remaining leaf sheath and stem material. Each component was then dried separately and weighed.

A more detailed examination of the live leaves was also carried out but the approach varied somewhat in each of the experiments. In the first 3 experiments, there was no direct means available of measuring leaf area. Consequently, leaf length was selected as an easily assessable parameter. In each experiment, 4 plants were selected at random from the central 8 and the length of each leaf recorded. In the final experiment, a leaf area meter became available by courtesy of the

Institute of Tree Biology and it was then possible to measure the leaf area of all experimental plants quickly and easily. In the first 3 experiments, it was also noted whether the leaves measured for length were flat or rolled. It seemed that there was a higher frequency of rolled leaves in the wind exposed plants which suggested that a water stress might have been induced by the action of wind.

Another aspect examined was the frequency of occurrence of transverse fold lines on the leaves. A transverse fold line seems to result from the whiplash motion of the leaf in the wind and, once formed, may then become an axis about which the rest of the leaf can flutter. In addition to the obvious fold lines, there were frequently minor transverse markings on the leaves. Any such markings which did not extend completely across the leaf were ignored in counting. In the first 3 experiments, the leaves were examined for transverse fold lines when their lengths were measured, and so again, only 4 plants in each box were assessed. In the final experiment, all the central 8 plants were examined for transverse fold lines before separating into the various components. The final harvests in all experiments were arduous and lasted over several days. The wind tunnel was kept in operation until the end of the harvest and the replicates were removed at random as required. Because of this, the final number of tillers may not quite follow the trend of the weekly tiller counts as the time interval between the penultimate count and the final one might have been other than a week and would have been designated as the middle day of the final harvest.

8.6 Evaluation of results

The results from the yield experiments can be divided into two groups, the weekly tiller counts and the larger number of parameters such as dry weights, which were obtained during the final harvest.

The weekly tiller counts provided the only means by which the effect of wind on a rate process could be assessed. Wadsworth (1959) has stressed the value of growth rates but, although desirable, it was not possible to arrange for the necessary sequential yield harvests in these experiments.

In order to find out whether the differences in yield were really a reflection of differences in growth rates rather than in initial sizes, the rates of increase of tiller numbers per plant were examined. In certain situations, it may be possible to transform such data to produce linear relationships and then to examine for any differences between the gradients of the lines. Unfortunately, in these experiments the data proved difficult to linearize. Plots of log. data against time, log. log. data against time, log. data against log. time, log. log. data against log. time and log. data against the reciprocal of time all proved to be ineffective. This approach was therefore abandoned and instead, the relative rates of tiller increase per week were calculated using the same adaptation of the growth rate formula as described in Chapter 3. As previously explained, due to the problem of fixing an average date for the final harvests, the figures for the final growth periods were doubtful as absolute values but still of use for comparative purposes.

The results from the final harvests of each of the 4 yield experiments constitute a large volume even of primary data. To process this data and to generate the derived data, computer programmes were written and run at the Edinburgh Regional Computing Centre using either an IBM 370/155 or an ICL 4-75 computer. As each experiment was of the same design i.e. a 2 x 2 x 2 factorial, the data were generated in a form easily useable for subsequent statistical analysis. Analyses of variance on appropriate parameters were carried out using a standard programme, BMD 02V, part of a package produced by the University of

Table 8.1 Example of detailed data and analysis of variance.
Wind Tunnel Yield Experiment 4. Final harvest.

Mean number of tillers per plant.

	W_1				W_2			
	P_1N_1	P_1N_2	P_2N_1	P_2N_2	P_1N_1	P_1N_2	P_2N_1	P_2N_2
REP 1	7.000	21.125	8.500	20.875	7.250	14.750	6.625	16.875
REP 2	7.125	20.375	5.625	17.125	6.000	16.000	6.875	16.875
REP 3	6.625	17.375	5.625	20.125	7.000	17.750	5.875	19.250
REP 4	6.875	19.125	8.375	20.750	6.125	14.500	8.000	15.500
REP 5	7.625	17.000	5.500	20.875	5.750	15.875	7.500	18.625
MEANS	7.050	19.000	6.725	19.950	6.425	15.775	6.975	17.425

VARIABLE MEANS

	W	P	N
LEVEL 1	13.181	12.063	6.794
LEVEL 2	11.650	12.769	18.037

WIND EXPOSED PLANTS AS % OF CONTROLS ($W_2/W_1 \times 100$)

P_1N_1	P_1N_2	P_2N_1	P_2N_2
91.21	83.05	103.72	87.37

ANALYSIS OF VARIANCE

SOURCE OF VARIATION	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES	F RATIO	LEVEL OF SIGNIFICANCE (%).
W	1	23.447	23.447	13.923	0.1
P	1	4.988	4.988	2.962	10.0
N	1	1264.217	1264.217	750.723	0.1
WxP	1	1.550	1.550	0.920	N.S.
WxN	1	18.059	18.059	10.724	0.5
PxN	1	3.527	3.527	2.094	N.S.
WxPxN	1	0.014	0.014	0.008	N.S.
WITHIN REPS	32	53.894	1.684		
TOTAL	39	1369.695			

$$\text{L.S.D.} = 2.042 \sqrt{\frac{2 \times 1.684}{5}} = 1.68 \text{ Tillers per plant.}$$

California at Los Angeles (Dixon, 1970).

In the analyses of variance a level of significance of 10% was accepted. All parameters showing a significant effect of wind overall were then examined for least significant differences using a 5% level of significance.

Because of the large bulk of data which would otherwise have to be presented, the results of the final harvests are given in summary and sometimes histogram form in the appropriate chapters. A full example of the detailed data and the analysis of variance of the final number of tillers per plant in the fourth wind tunnel yield experiment is given in Table 8.1.

8.7 Conclusions

The conclusions from each experiment are outlined very briefly at the ends of the appropriate chapters. To obtain an overall picture of the 4 experiments, further consideration is given to the effects of wind in particular, in Chapter 13.

CHAPTER 9.

WIND TUNNEL YIELD EXPERIMENT 1.

9.1 Introduction

The object of this experiment was to assess the effect of wind of a low level of turbulence on the growth of S.170 Festuca arundinacea Schreb. grown at different levels of phosphorus and nitrogen. The experimental design was factorial with 2 levels of wind, 2 levels of phosphorus, 2 levels of nitrogen and 5 replicates.

9.2 Experimental procedure

In this first wind tunnel experiment, the levels of phosphorus applied initially to the peat/sand mix were equivalent to 5 p.p.m. and 15 p.p.m. Other than potassium nitrate, no extra source of nitrogen was added and hoof and horn was excluded from the mixture.

On 16.11.1970, the seeds were sown in a shallow tray and allowed to germinate. They were transplanted into the wind tunnel boxes on 2.12.1970, watered, and then allowed to grow in the greenhouse for 6 weeks. On 13.1.1971, they were removed to a growth room with the temperature set at $10^{o}C$. The temperature was reduced to $4^{o}C$ on 18.1.1971. On 20.1.1971, the plants were clipped to 8 cm and the lights in the room adjusted to give a 12-hour day from 06.00 to 18.00. On 1.2.1971, the levels of nutrients were supplemented by an equivalent of 30 p.p.m. of phosphorus and 600 p.p.m. of nitrogen. Thus the final nutrient levels were:

P_1	5 p.p.m.
P_2	45 p.p.m.
N_1	21 p.p.m.
N_2	621 p.p.m.

The first tiller count took place on 2.2.1971, although the experiment itself did not start until 5.2.1971. Thereafter, tillers were counted each week until the end of the experiment. After the plants had been exposed in the wind tunnel for 55 days, the experiment was terminated, replicate by replicate, with a destructive harvest. This harvest started on 30.3.1971 and finished on 7.4.1971 giving an average date of 3.4.1971.

It appeared from the general growth of the grass that the nutrient levels chosen were both realistic and sufficiently different to produce quite distinct growth responses. Unfortunately it seems likely that the application of an equivalent of 600 p.p.m. nitrogen on a single occasion was excessive. Despite the use of ammonium nitrate, which should have been less toxic than urea, the treated plants tended to show necrosis of the ends of the leaves, particularly those which had been cut during the trimming. Apart from one leaf which died, these effects were of short duration and the faster growth rate of the N_2 plants soon became obvious.

Three weeks after the start of the experiment, due to the increase in height of the plants, the top of the canopy was adjusted to its original height in relation to the light source by lowering the working section by 5 cm. The gap that this caused was sealed up by the use of strips of hardboard. When raising the floor of the working section, the final adjustments were made manually so that the tops of the hardboard strips were in contact with the walls of the working section. The rapid growth in height of the canopy later cast doubts on the wisdom of this provision; to have maintained this objective, the floor of the working section would eventually have had to have been lowered by about 15 cm.

During the experiment, some difficulties were experienced with the loss of temperature control by the wind tunnel, but these effects were of short duration and were corrected as the boxes were changed over and usually much earlier. On one occasion, due to the failure of water supplies in the building, the temperature rose to 21°C before correction. It was more difficult to maintain the growth room at a temperature of 5°C. This was due to the accumulation of ice on the heat exchanger, which, about twice a week, caused a loss of temperature control. When this happened, it was necessary to raise the room temperature briefly to 15 - 20°C to ensure complete de-icing. This exercise was unfortunate, but unavoidable, although both treatments were probably affected to an equal extent. With experience, this difficulty was overcome by anticipating when de-icing would be necessary.

9.3 Results of the weekly tiller counts

The weekly increases in numbers of tillers expressed on a per-plant basis are shown for each nutrient treatment in Figures 9.1, 9.2, 9.3 and 9.4. Each value is the mean of the 5 replicates and thus of 40 plants. The most pronounced effect of wind was in the P_2N_2 treatment, where plants subjected to the higher wind speed had 18.13% fewer tillers by the final harvest. In addition, this treatment had the most rapid rate of increase overall. The P_1N_2 treatment showed a similar, but less-pronounced trend, whilst the P_2N_1 and P_1N_1 treatments showed little discernable effect of wind. The difficulty of interpreting such results because of initial differences in numbers of tillers has already been stressed and in the P_1N_2 and P_2N_2 treatments, the final results may be partly a reflection of the initial values. It should be noted that, in the final harvest, the effect of wind was only significant in the P_2N_2 treatment.

FIGURE 9.1
WIND TUNNEL YIELD EXPERIMENT 1

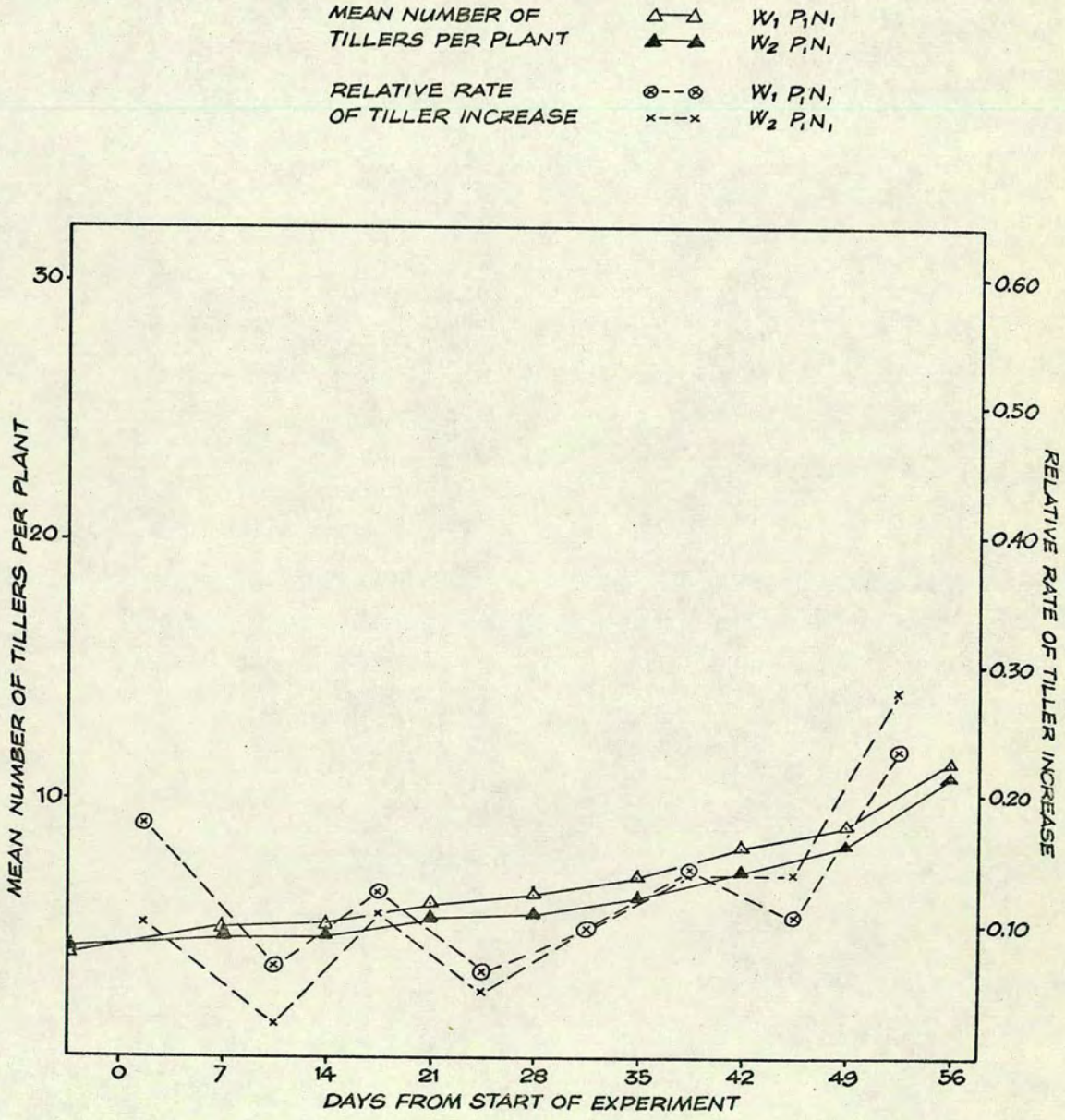


FIGURE 9.2
WIND TUNNEL YIELD EXPERIMENT 1

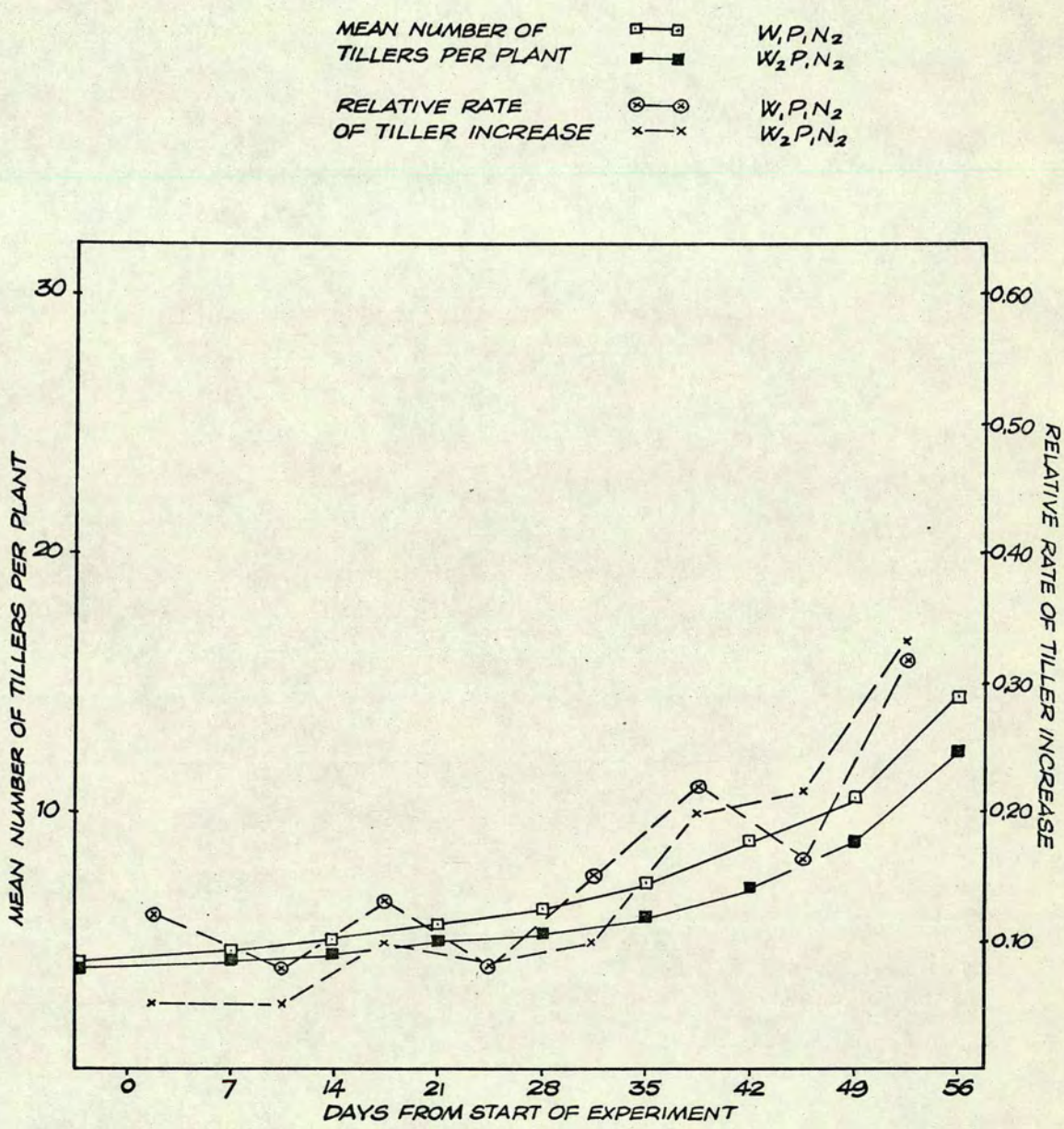


FIGURE 9,3
WIND TUNNEL YIELD EXPERIMENT 1

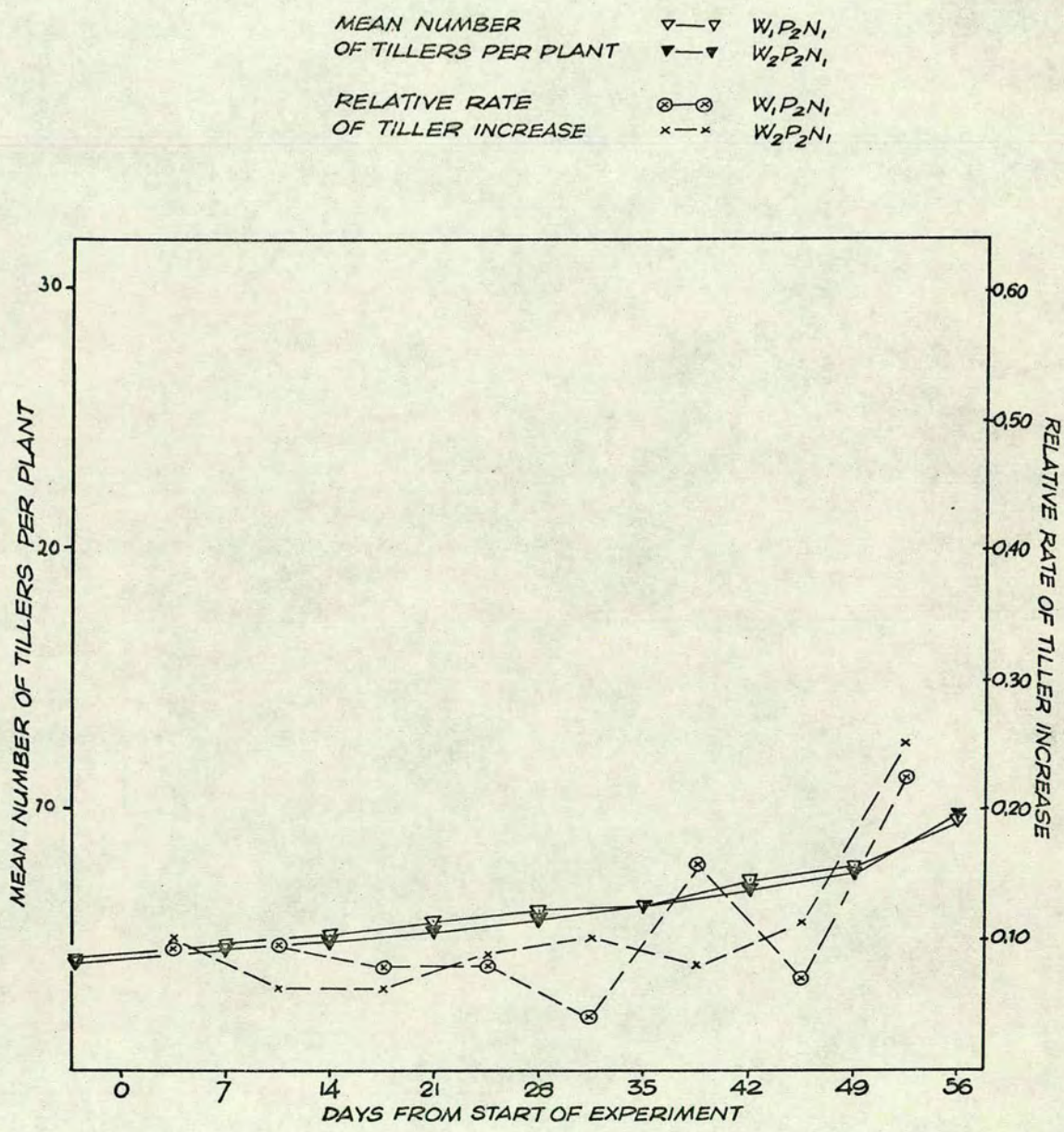
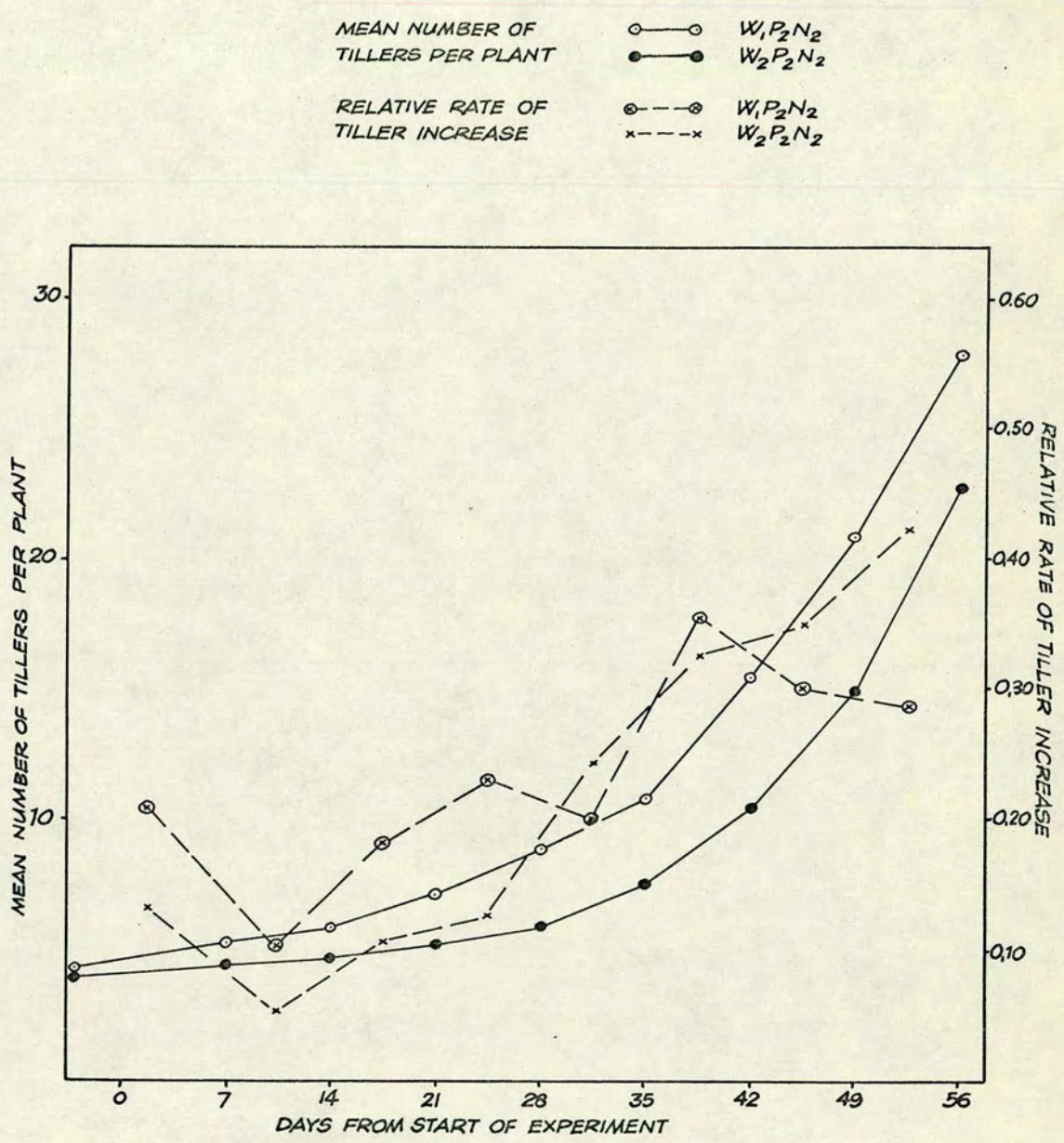


FIGURE 9.4 WIND TUNNEL YIELD EXPERIMENT 1



The relative rates of tiller increase during the intervals between counts are also shown in Figures 9.1, 9.2, 9.3 and 9.4 . A very interesting feature was the higher initial growth rate in the W_1 plants followed, apart from a perturbation in the sixth interval, by a reversal towards the end of the experiment when the W_2 plants were growing faster. An initial interpretation would be that the W_1 plants had reached their optimum leaf area index more rapidly than the W_2 plants and that after this the growth rate declined. If this were the case, the effect should have appeared first in the P_2N_2 treatment, but this was not so; even the P_2N_1 treatment showed the same trend. In fact this effect generally seems to have occurred towards the end of the experiment for reasons which are not clear.

9.4 Results of the final harvest

Throughout this experiment, it had been suspected that the $W_2P_1N_1$ treatment in replicate 1 had a higher nitrogen level than originally intended. This was confirmed by an examination of the results of the analysis of the border plants for total nitrogen content thus suggesting an error in fertilizer application. In such situations missing plot procedures can be used, but the problem with the BMD 02V programme is that no such facility is available. With 5 replicates and this experimental design, it was considered unlikely that one particular value would greatly affect the overall results. This was tested by substituting the mean value of the remaining 4 correct plots in the analysis and then examining the data for any differences in statistical significance. The comparison between the original and modified data for those parameters in which wind had a significant effect overall is shown in Table 9.1. It can be seen that the level of significance was increased in 8 out of 10 parameters by this procedure, but the patterns for the

WIND TUNNEL YIELD EXPERIMENT 1.

Table 9.1 Comparison of analyses of variance with original (A) and modified (B) data:Final harvest.

	Source of variation													
	W		P		N		WxP		WxN		PxN		WxPxN	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
TOTAL DRY WEIGHT PER PLANT														
F.RATIO	9.06	10.78	17.08	19.63	78.82	86.06	1.59	1.17	3.64	3.03	37.33	36.37	1.78	2.47
LEVEL OF SIGNIFICANCE %	1.0	0.5	0.1	0.1	0.1	0.1	N.S.	N.S.	10.0	10.0	0.1	0.1	N.S.	N.S.
DRY WEIGHT OF SHOOTS PER PLANT														
F.RATIO	11.94	16.65	38.34	49.14	212.00	254.98	2.50	1.72	6.66	5.67	74.61	78.59	2.75	4.65
LEVEL OF SIGNIFICANCE	0.5	0.1	0.1	0.1	0.1	0.1	N.S.	N.S.	2.5	2.5	0.1	0.1	N.S.	5.0
DRY WEIGHT OF LEAF SHEATH AND STEM PER PLANT														
F.RATIO	7.76	11.94	21.76	30.27	132.58	167.92	1.12	0.53	4.47	3.52	49.77	52.63	1.00	2.30
LEVEL OF SIGNIFICANCE	1.0	0.5	0.1	0.1	0.1	0.1	N.S.	N.S.	5.0	10.0	0.1	0.1	N.S.	N.S.
DRY WEIGHT OF LIVE LEAVES PER PLANT														
F.RATIO	9.19	13.33	39.19	50.68	203.84	247.43	3.12	2.26	5.70	4.71	69.80	73.58	3.23	5.41
LEVEL OF SIGNFICANCE	0.5	0.1	0.1	0.1	0.1	0.1	10.0	N.S.	2.5	5.0	0.1	0.1	10.0	5.0
TOTAL LEAF LENGTH PER PLANT														
F.RATIO	12.26	17.98	36.37	48.91	112.16	142.95	6.29	5.29	7.02	6.02	43.26	45.28	7.98	12.28
LEVEL OF SIGNIFICANCE	0.5	0.1	0.1	0.1	0.1	0.1	2.5	5.0	2.5	2.5	0.1	0.1	1.0	0.5
NUMBER OF TRANSVERSE FOLD LINES PER PLANT														
F.RATIO	5.02	4.97	1.41	1.44	2.26	2.30	1.17	1.14	0.51	0.53	0.58	0.61	0.51	0.53
LEVEL OF SIGNIFICANCE	5.0	5.0	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

WIND TUNNEL YIELD EXPERIMENT 1.

Table 9.1 Comparison of analyses of variance with original (A) and modified (B) data : Final harvest (continued).

	Source of variation													
	W		P		N		WxP		WxN		PxN		WxPxN	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
NUMBER OF LIVE LEAVES PER PLANT														
F.RATIO	4.92	7.84	33.44	44.22	96.09	120.28	1.52	0.85	2.34	1.55	54.44	57.13	1.82	3.4
LEVEL OF SIGNIFICANCE	5.0	1.0	0.1	0.1	0.1	0.1	N.S.	N.S.	N.S.	N.S.	0.1	0.1	N.S.	10.0
NUMBER OF TILLERS PER PLANT														
F.RATIO	4.78	8.17	37.16	51.17	102.93	134.64	0.37	0.05	3.47	2.53	54.46	58.58	1.03	2.4
LEVEL OF SIGNIFICANCE	5.0	1.0	0.1	0.1	0.1	0.1	N.S.	N.S.	10.0	N.S.	0.1	0.1	N.S.	N.S
TOTAL LEAF LENGTH PER TILLER														
F.RATIO	5.50	5.86	3.08	3.35	40.64	41.73	2.31	2.11	0.02	0.01	4.65	4.37	2.84	3.1
LEVEL OF SIGNIFICANCE	2.5	2.5	10.0	10.0	0.1	0.1	N.S.	N.S.	N.S.	N.S.	5.0	5.0	N.S.	10.0
NITROGEN CONTENT AS PERCENTAGE OF SHOOT DRY WEIGHT														
F.RATIO	3.64	7.67	24.20	278.96	767.65	6674.18	0.00	6.57	0.00	6.60	47.76	290.41	1.15	0.1
LEVEL OF SIGNIFICANCE	10.0	1.0	0.1	0.1	0.1	0.1	N.S.	2.5	N.S.	2.5	0.1	0.1	N.S.	N.S

N.S. : No significance (for levels greater than 10%).

first order and second order interactions are slightly more confused. In none of the other parameters was the effect of wind changed from being significant to not being significant through the use of the modified data. It was therefore decided to use the modified data and the full results are shown in Tables 9.2., 9.3 and 9.4. Those parameters of particular interest are shown in histogram form in Figure 9.5.

Examination of the results in detail shows that the total dry matter production per plant was decreased by wind, increased by phosphorus and increased by nitrogen. The W x P interaction was not significant, but the W x N interaction was significant at the 10% level. The L.S.D. calculation shows that the overall effect of wind in fact only applied to the P_2N_2 treatments where wind caused a 19.83% reduction compared to the controls.

From the practical viewpoint, probably the effects on shoot dry weight are of most interest. Overall production was decreased 13.60% by wind, increased 28.43% by phosphorus and increased 79.04% by nitrogen, each effect being significant at 0.1%. In the P_2N_2 treatment, the reduction due to wind amounted to 20.20%. The W x N and W x P x N interactions were also significant at the 2.5% and 5% levels respectively.

The dry weight of roots was not significantly affected by wind, although in all cases there was a reduction which, in the P_2N_2 treatment amounted to 17.46%. Nitrogen had a significant effect at 0.5%.

The shoot production was divided into dead leaves, live leaves and the remaining stems and leaf sheaths. In addition to the actual dry weights, the proportion that each component formed of the whole was also considered.

The dry weight of dead leaves was only slightly affected by wind, but not significantly. The proportion was also not significantly

WIND TUNNEL YIELD EXPERIMENT 1.

Table 9.2 Overall experimental effects : Final harvest

Component of yield	Variable	Level 1	Level 2	% Change
TOTAL DRY WEIGHT PER PLANT (mg)	W	645	565	- 12.40
	P	551	659	+ 19.60
	N	492	718	+ 45.94
DRY WEIGHT OF SHOOTS PER PLANT (mg)	W	500	432	- 13.60
	P	408	524	+ 28.43
	N	334	598	+ 79.04
DRY WEIGHT OF ROOTS PER PLANT (mg)	W	145	133	- 8.28
	P	143	135	- 5.59
	N	158	119	- 24.68
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	W	29.8	29.3	- 1.68
	P	31.5	27.6	- 2.38
	N	33.4	25.7	- 3.05
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	W	7.14	7.73	+ 8.26
	P	8.10	6.77	- 16.42
	N	10.15	4.72	- 53.50
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	W	216	179	- 17.13
	P	162	234	+ 44.44
	N	118	277	+134.75
DRY WEIGHT OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	W	40.87	39.81	- 2.59
	P	39.02	41.67	+ 6.79
	N	35.14	45.54	+ 29.60

Table 9.2 Overall experimental effects : Final harvest (continued)

Component of yield	Variable	Level 1	Level 2	% Change
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	W	254	224	- 11.81
	P	215	263	+ 22.33
	N	182	295	+ 62.09
DRY WEIGHT OF LEAF SHEATHS AND STEMS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	W	51.99	52.46	+ 0.90
	P	52.89	51.57	- 2.50
	N	54.71	49.74	- 9.08
ROOT : SHOOT RATIO	W	0.37	0.38	+ 2.70
	P	0.40	0.35	- 12.50
	N	0.53	0.22	- 58.49
TOTAL LEAF LENGTH PER PLANT (mm)	W	1968	1456	- 26.02
	P	1290	2134	+ 65.43
	N	990	2434	+145.86
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	W	0.87	1.40	+ 60.92
	P	0.99	1.28	+ 29.29
	N	0.95	1.31	+ 37.89
NUMBER OF LIVE LEAVES PER PLANT	W	26.23	21.46	- 18.19
	P	18.18	29.51	+ 62.32
	N	14.48	33.21	+129.35
INDIVIDUAL LEAF DRY WEIGHT (mg)	W	8.4	8.6	+ 2.38
	P	9.0	8.1	- 10.00
	N	8.3	8.7	+ 4.82
INDIVIDUAL LEAF LENGTH (mm)	W	72	69	- 4.17
	P	70	71	+ 1.43
	N	67	75	+ 11.94

Table 9.2 Overall experimental effects : Final harvest (continued)

Component of yield	Variable	Level 1	Level 2	% Change
NUMBER OF DEAD LEAVES PER PLANT	W	5.56	5.37	- 3.42
	P	5.59	5.35	- 4.29
	N	5.86	5.08	- 13.31
NUMBER OF TILLERS PER PLANT	W	15.84	13.54	- 14.62
	P	11.81	17.58	+ 48.86
	N	10.01	19.37	+ 93.51
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER (mg)	W	44.5	45.1	+ 1.35
	P	48.5	41.1	- 15.26
	N	50.6	39.0	- 22.92
DRY WEIGHT PER TILLER (mg)	W	32.9	33.3	+ 1.22
	P	35.4	30.9	- 12.71
	N	34.2	32.1	- 6.14
DRY WEIGHT OF LEAVES PER TILLER (mg)	W	13.3	13.1	- 1.50
	P	13.7	12.7	- 7.30
	N	11.9	14.5	+ 21.85
NUMBER OF LIVE LEAVES PER TILLER	W	1.60	1.53	- 4.37
	P	1.54	1.59	+ 3.25
	N	1.45	1.68	+ 15.86
TOTAL LEAF LENGTH PER TILLER (mm)	W	115	105	- 8.70
	P	106	114	+ 7.55
	N	96	124	+ 29.17
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	W	0.89	1.04	+ 17.00
	P	0.67	1.26	+ 88.91
	N	0.90	1.03	+ 14.83

Table 9.2 Overall experimental effects : Final harvest

Component of yield	Variable	Level 1	Level 2	% Change
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	W	0.33	0.33	+ 1.85
	P	0.16	0.49	+204.94
	N	0.30	0.36	+ 20.13
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	W	2.69	2.79	+ 3.72
	P	2.43	3.04	+ 25.10
	N	1.25	4.23	+228.40

WIND TUNNEL YIELD EXPERIMENT 1.

Table 9.3 The effect of exposure to wind on yields : Final harvest.

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
TOTAL DRY WEIGHT PER PLANT (mg)	P_1N_1	536	487	- 9.14	+	99 mg
	P_1N_2	619	562	- 9.21		
	P_2N_1	485	460	- 5.15		
	P_2N_2	938	752	- 19.83		
DRY WEIGHT OF SHOOTS PER PLANT (mg)	P_1N_1	371	328	- 11.59	+	68 mg
	P_1N_2	492	442	- 10.16		
	P_2N_1	326	312	- 4.29		
	P_2N_2	812	648	- 20.20		
DRY WEIGHT OF ROOTS PER PLANT (mg)	P_1N_1	166	158	- 4.82	-	-
	P_1N_2	128	119	- 7.03		
	P_2N_1	160	148	- 7.50		
	P_2N_2	126	104	- 17.46		
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	P_1N_1	32.9	34.7	+ 5.50	-	-
	P_1N_2	30.5	28.1	- 7.90		
	P_2N_1	33.4	32.8	- 1.80		
	P_2N_2	22.5	21.8	- 3.10		
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	P_1N_1	9.11	10.56	+ 15.92	-	-
	P_1N_2	6.41	6.32	- 1.40		
	P_2N_1	10.25	10.68	+ 4.20		
	P_2N_2	2.78	3.36	+ 20.86		
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	P_1N_1	137	114	- 16.79	+	41 mg
	P_1N_2	208	188	- 9.62		
	P_2N_1	114	108	- 5.26		
	P_2N_2	406	308	- 24.16		

Table 9.3 The effect of exposure to wind on yields : Final harvest (continued)

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
DRY WEIGHT OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	P_1N_1	36.51	34.72	- 4.90	-	-
	P_1N_2	42.07	42.76	+ 1.64		
	P_2N_1	35.05	34.28	- 2.20		
	P_2N_2	49.85	47.47	- 4.77		
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	P_1N_1	200	180	- 10.00	+	36 mg
	P_1N_2	253	226	- 10.67		
	P_2N_1	178	171	- 3.93		
	P_2N_2	384	318	- 17.19		
DRY WEIGHT OF LEAF SHEATHS AND STEMS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	P_1N_1	54.38	54.73	+ 0.64	-	-
	P_1N_2	51.52	50.91	- 1.18		
	P_2N_1	54.70	55.05	+ 0.64		
	P_2N_2	47.36	49.16	+ 3.80		
ROOT : SHOOT RATIO	P_1N_1	0.50	0.54	+ 8.00	-	-
	P_1N_2	0.28	0.29	+ 3.57		
	P_2N_1	0.55	0.54	- 1.82		
	P_2N_2	0.16	0.17	+ 6.25		
TOTAL LEAF LENGTH PER PLANT (mm)	P_1N_1	1155	794	- 31.26	+	493 mm
	P_1N_2	1659	1552	- 6.45		
	P_2N_1	1041	791	- 24.02		
	P_2N_2	4017	2508	- 37.57		
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	P_1N_1	0.50	0.94	+ 88.00	+	0.97
	P_1N_2	0.70	1.83	+161.43		
	P_2N_1	0.05	1.33	+2560.00		
	P_2N_2	1.23	1.50	+ 21.95		

Table 9.3 The effect of exposure to wind on yields : Final harvest (continued)

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
NUMBER OF LIVE LEAVES PER PLANT	P_1N_1	17.38	13.13	- 24.45	+	6.96
	P_1N_2	22.18	20.03	- 9.69		
	P_2N_1	14.23	13.18	- 7.38		
	P_2N_2	51.15	39.50	- 22.78		
INDIVIDUAL LEAF DRY WEIGHT (mg)	P_1N_1	8.2	8.7	+ 6.10	-	-
	P_1N_2	9.3	9.6	+ 3.23		
	P_2N_1	8.0	8.2	+ 2.50		
	P_2N_2	8.0	8.0	+ 0.0		
INDIVIDUAL LEAF LENGTH (mm)	P_1N_1	67	64	- 4.48	-	-
	P_1N_2	75	74	- 1.33		
	P_2N_1	69	67	- 2.90		
	P_2N_2	78	72	- 7.69		
NUMBER OF DEAD LEAVES PER PLANT	P_1N_1	5.85	5.72	- 2.22	-	-
	P_1N_2	5.48	5.30	- 3.28		
	P_2N_1	6.08	5.80	- 4.61		
	P_2N_2	4.85	4.68	- 3.51		
NUMBER OF TILLERS PER PLANT	P_1N_1	11.28	9.16	- 18.79	+	3.29
	P_1N_2	14.48	12.33	- 14.85		
	P_2N_1	9.78	9.85	+ 0.72		
	P_2N_2	27.85	22.80	- 18.13		
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER (mg)	P_1N_1	51.5	53.4	+ 3.69	-	-
	P_1N_2	43.1	45.9	+ 6.50		
	P_2N_1	49.8	47.6	- 4.42		
	P_2N_2	33.7	33.3	- 1.19		

Table 9.3 The effect of exposure to wind on yields : Final harvest (continued)

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
DRY WEIGHT PER TILLER (mg)	P_1N_1	35.0	36.2	+ 3.43	-	-
	P_1N_2	34.2	36.2	+ 5.85		
	P_2N_1	33.4	32.2	- 3.59		
	P_2N_2	29.1	28.7	- 1.37		
DRY WEIGHT OF LIVE LEAVES PER TILLER (mg)	P_1N_1	12.5	12.5	0.00	-	-
	P_1N_2	14.4	15.3	+ 6.25		
	P_2N_1	11.7	10.9	- 6.84		
	P_2N_2	14.5	13.6	- 6.21		
NUMBER OF LIVE LEAVES PER TILLER	P_1N_1	1.54	1.44	- 6.49	-	-
	P_1N_2	1.55	1.62	+ 4.52		
	P_2N_1	1.46	1.34	- 8.22		
	P_2N_2	1.83	1.71	- 6.56		
TOTAL LEAF LENGTH PER TILLER (mm)	P_1N_1	102	91	- 10.78	+	17 mm
	P_1N_2	114	117	+ 2.63		
	P_2N_1	100	91	- 9.00		
	P_2N_2	144	120	- 16.67		
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	P_1N_1	0.87	0.91	+ 5.18	-	-
	P_1N_2	0.36	0.52	+ 44.35		
	P_2N_1	0.86	0.95	+ 9.76		
	P_2N_2	1.46	1.78	+ 21.66		
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	P_1N_1	0.18	0.17	- 2.82	-	-
	P_1N_2	0.15	0.15	+ 1.34		
	P_2N_1	0.41	0.43	+ 4.12		
	P_2N_2	0.56	0.57	+ 1.78		
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	P_1N_1	1.29	1.22	- 5.43	+	0.15%
	P_1N_2	3.57	3.65	+ 2.24		
	P_2N_1	1.20	1.29	+ 7.50		
	P_2N_2	4.69	4.99	+ 6.40		

WIND TUNNEL YIELD EXPERIMENT 1.

Table 9.4 Summary of Analyses of Variance : Final harvest.

Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
TOTAL DRY WEIGHT PER PLANT	F	10.78	19.63	86.06	1.17	3.03	36.37	2.47
	S	0.5	0.1	0.1	N.S.	10.0	0.1	N.S.
DRY WEIGHT OF SHOOTS PER PLANT	F	16.65	49.14	254.98	1.72	5.67	78.59	4.65
	S	0.1	0.1	0.1	N.S.	2.5	0.1	5.0
DRY WEIGHT OF ROOTS PER PLANT	F	1.06	0.48	10.40	0.15	0.06	0.00	0.05
	S	N.S.	N.S.	0.5	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT OF DEAD LEAVES PER PLANT	F	0.09	5.55	21.60	0.01	0.46	3.81	0.38
	S	N.S.	5.0	0.1	N.S.	N.S.	10.0	N.S.
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	F	1.61	8.16	135.18	0.03	0.55	17.64	0.82
	S	N.S.	1.0	0.1	N.S.	N.S.	0.1	N.S.
DRY WEIGHT OF LIVE LEAVES PER PLANT	F	13.33	50.68	247.43	2.26	4.71	73.58	5.41
	S	0.1	0.1	0.1	N.S.	5.0	0.1	5.0
DRY WEIGHTS OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	F	1.01	6.31	97.16	0.24	0.04	11.62	0.94
	S	N.S.	2.5	0.1	N.S.	N.S.	0.5	N.S.
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT	F	11.94	30.27	167.92	0.53	3.52	52.63	2.30
	S	0.5	0.1	0.1	N.S.	10.0	0.1	N.S.
DRY WEIGHTS OF LEAF SHEATHS AND STEMS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	F	0.26	2.05	29.24	0.43	0.02	3.17	0.43
	S	N.S.	N.S.	0.1	N.S.	N.S.	10.0	N.S.

Table 9.4 Summary of analyses of variance : Final harvest (continued)

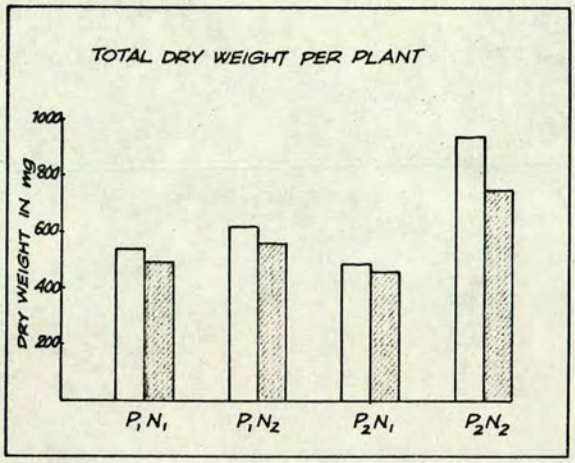
Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
ROOT : SHOOT RATIO	F	0.09	1.85	75.03	0.13	0.00	3.81	0.07
	S	N.S.	N.S.	0.1	N.S.	N.S.	10.0	N.S.
TOTAL LEAF LENGTH PER PLANT	F	17.98	48.91	142.95	5.29	6.02	45.28	12.28
	S	0.1	0.1	0.1	5.0	2.5	0.1	0.5
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	F	4.97	1.44	2.30	1.14	0.53	0.61	0.53
	S	5.0	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
NUMBER OF LIVE LEAVES PER PLANT	F	7.84	44.22	120.28	0.85	1.55	57.13	3.47
	S	1.0	0.1	0.1	N.S.	N.S.	0.1	10.0
INDIVIDUAL LEAF DRY WEIGHT	F	0.65	6.91	1.79	0.18	0.08	2.75	0.02
	S	N.S.	2.5	N.S.	N.S.	N.S.	N.S.	N.S.
INDIVIDUAL LEAF LENGTH	F	1.94	0.37	14.71	0.10	0.05	0.22	0.65
	S	N.S.	N.S.	0.1	N.S.	N.S.	N.S.	N.S.
NUMBER OF DEAD LEAVES PER PLANT	F	0.41	0.64	7.08	0.02	0.00	1.73	0.02
	S	N.S.	N.S.	2.5	N.S.	N.S.	N.S.	N.S.
NUMBER OF TILLERS PER PLANT	F	8.17	51.17	134.64	0.05	2.53	58.58	2.47
	S	1.0	0.1	0.1	N.S.	N.S.	0.1	N.S.
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER	F	0.06	10.16	24.74	0.60	0.08	2.43	0.01
	S	N.S.	0.5	0.1	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT PER TILLER	F	0.08	11.85	2.64	0.81	0.09	1.74	0.00
	S	N.S.	0.5	N.S.	N.S.	N.S.	N.S.	N.S.

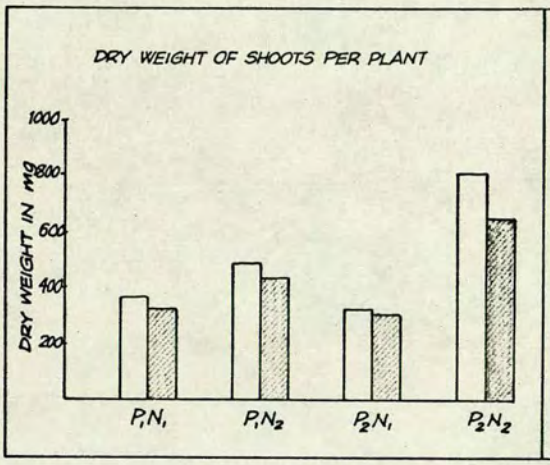
Table 9.4 Summary of analyses of variance : Final harvest (continued)

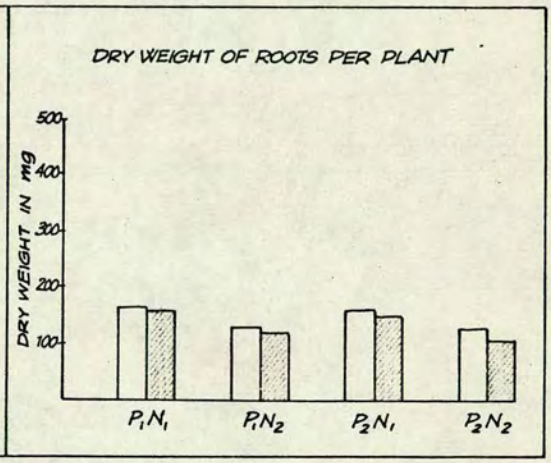
Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
DRY WEIGHT OF LIVE LEAVES PER TILLER	F	0.24	6.39	40.99	2.89	0.24	0.22	0.45
	S	N.S.	2.5	0.1	10.0	N.S.	N.S.	N.S.
NUMBER OF LIVE LEAVES PER TILLER	F	2.82	1.49	31.53	1.60	1.08	11.66	1.11
	S	N.S.	N.S.	0.1	N.S.	N.S.	0.5	N.S.
TOTAL LEAF LENGTH PER TILLER	F	5.86	3.35	41.73	2.11	0.01	4.37	3.10
	S	2.5	10.0	0.1	N.S.	N.S.	5.0	10.0
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	F	1.25	19.14	0.97	0.13	0.41	18.35	0.05
	S	N.S.	0.1	N.S.	N.S.	N.S.	0.1	N.S.
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	F	0.98	2619.07	86.17	1.36	0.00	170.19	0.31
	S	N.S.	0.1	0.1	N.S.	N.S.	0.1	N.S.
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	F	7.67	278.96	6674.18	6.57	6.60	290.41	0.14
	S	1.0	0.1	0.1	2.5	2.5	0.1	N.S.

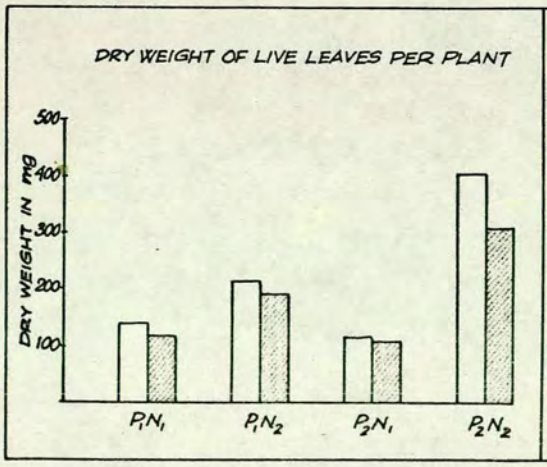
F : F ratio.
S : Level of significance (%).
N.S. : No significance (for levels greater than 10%).

FIGURE 9.5 WIND TUNNEL YIELD EXPERIMENT 1









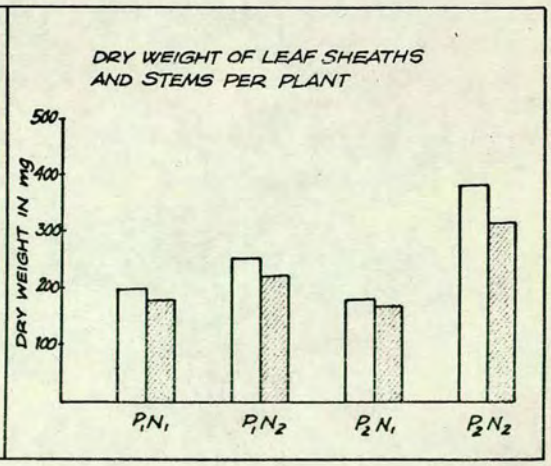
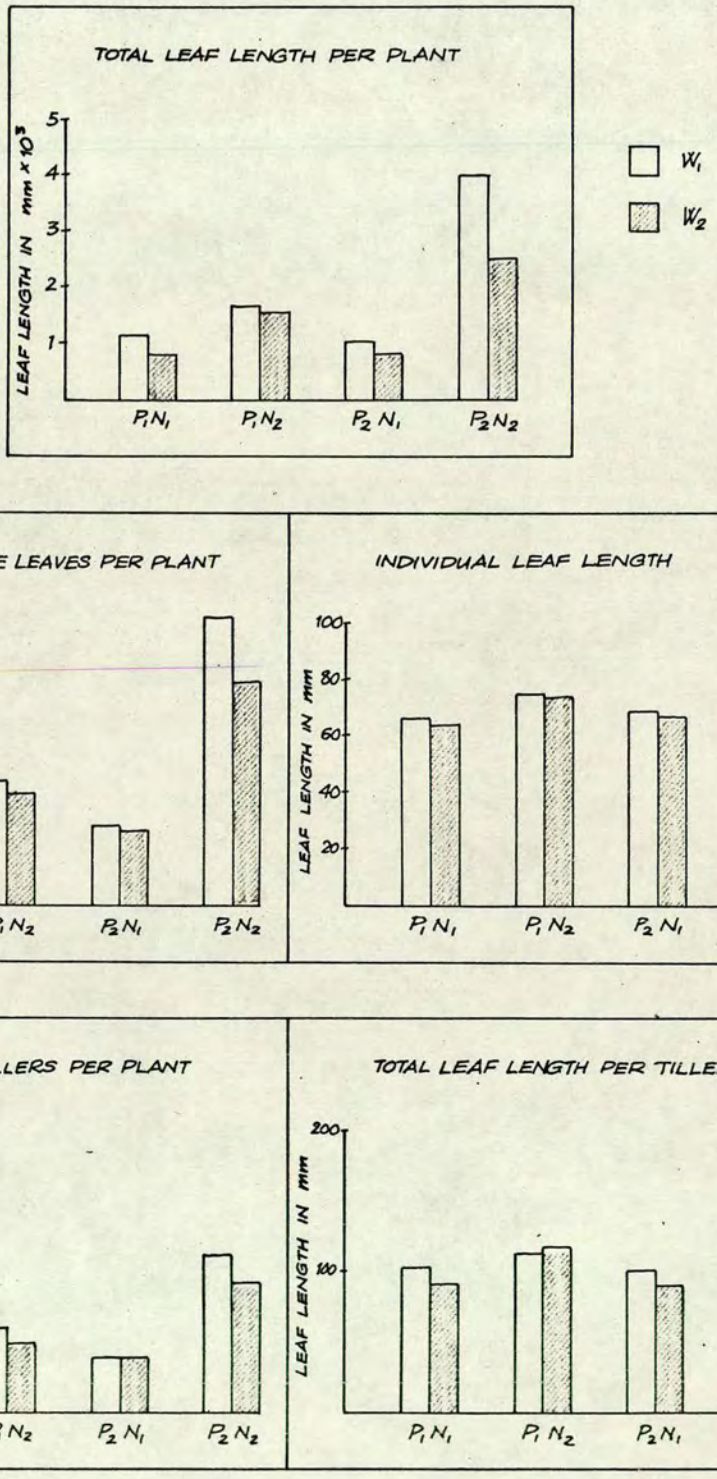


FIGURE 9,5 (CONTINUED) WIND TUNNEL YIELD EXPERIMENT I



affected by wind, although the $W_2P_2N_2$ treatment had a 20.86% higher proportion compared with the $W_1P_2N_2$ treatment. However, this large percentage difference was of little meaning biologically, since it represented an increase from only 2.78% to 3.36%.

The dry weight of live leaves was significantly reduced overall by wind, but again the L.S.D. value of 41 mg meant that this really only applied to the P_2N_2 treatment where the reduction was 24.16%. This parameter seemed to be especially responsive to all the imposed treatments; both nitrogen and phosphorus had significant effects, this being particularly true of nitrogen where there was an average overall increase of 134.75%. Also, the W x N interaction and the W x P x N interaction were both significant at the 5% level. Clearly, from an agricultural viewpoint, this is of interest since leaves form such a major proportion of edible production. Despite the large effect of wind on dry weights, the proportion of leaves in relation to total aerial production was only slightly reduced by wind, an effect which was not significant.

The remaining leaf sheaths and stems were also significantly reduced by exposure to wind, but again, an effect only applying to the P_2N_2 treatment where it represented a reduction of 17.19%. There was a marked effect of nitrogen and the W x N interaction was significant at 10%. Following the previous pattern, wind had little effect on the proportion of the aerial parts. Thus it seems that nitrogen was the main factor affecting the proportions of the components of aerial production.

Since wind significantly reduced aerial production, but not that of roots, an increase in the root:shoot ratio might have been expected. This would have supported the work by Whitehead (1962) on Helianthus annuus. However, this parameter was most strongly affected by nitrogen which caused a 58.49% reduction overall and was significant at 0.1%.

The effect of wind was itself not significant, nevertheless, except in the P_2N_1 treatment, increases of up to 8.00% occurred.

The total leaf length per plant was of interest, not only because of its importance to the grazing animal, but also because of its particular responsiveness to the various treatments applied. The overall effects, all of which were significant, showed that wind caused a 26.02% reduction, phosphorus a 65.43% increase and nitrogen a 145.86% increase in length. Also, the W x P, W x N and W x P x N interactions were all significant. In the P_2N_2 treatment, the reduction due to wind was 37.57%.

One reason for this sensitivity to wind could have been an increased number of transverse fold lines per plant, a factor which might have restricted the elongation of leaves. It can be seen that wind did increase the number of fold lines but the effect was only significant at 5%. Examination of the L.S.D. values shows that this only applied in the P_1N_2 and P_2N_1 treatments, whereas the only significant effect of wind on total leaf length occurred in the P_2N_2 treatment. Nevertheless, reductions in length due to wind of 6.45% in the P_1N_2 treatment and 24.02% in the P_2N_1 treatment still occurred, which would suggest that fold line frequency might have been at least partially causal. It should also be noted that,although not significant, the number of fold lines was increased 21.95% by wind in the P_2N_2 treatment, a further consideration in support of this hypothesis.

The effect of wind on the dry weight of leaves per plant may have been a reflection of differences between either the numbers of leaves per plant or the individual leaf dry weights or both. The number of leaves was in fact significantly reduced by wind, the L.S.D. value indicating that this only applied in the P_2N_2 treatment where it amounted to 22.78%. Nitrogen also had a strong influence and produced an overall increase of 129.35%. Wind resulted in a 2.38% increase overall in

individual leaf dry weight and a 4.17% overall decrease in individual leaf length, but neither effect was significant. Thus it would appear that the main consequence of exposure to wind was a reduction in leaf number rather than leaf length or dry weight. However, this does not contradict the hypothesis that transverse fold lines may have reduced leaf length, rather, it suggests that this aspect may have been relatively minor. It may still have been reflected in the small reduction of 7.69% which occurred in the P_2N_2 treatment.

The results show that wind also had no significant effect on the number of dead leaves.

One of the most important aspects determining the size of a grass plant is its ability to produce new tillers (Jewiss, 1972). Clearly, this is likely to have a profound effect on such parameters as the numbers of live and dead leaves as well as the total leaf length. The weekly tiller counts using the modified data have already been described, but the final numbers merit further exploration. Here wind reduced the number of tillers per plant significantly, but as in many other cases, nitrogen had a much more pronounced effect. The effect of wind was significant at 1.0% and reduced the number of tillers by 18.13% in the P_2N_2 treatment. Again this was the only treatment where the L.S.D. value was exceeded at the 5% level.

This raises the question of whether the individual tillers, although reduced in number by wind, was also reduced in size. Examination of the dry weight of all plant material per tiller; i.e. including roots, the dry weight per tiller, the dry weight of leaves per tiller and the number of leaves per tiller shows that none of these parameters were significantly affected by wind. However, the total leaf length per tiller was reduced by 16.67% in the P_2N_2 treatment, an effect significant at the

2.5% level. Such a reduction might have been expected from the increased fold line frequency noted previously.

Thus these results show that the number of tillers per plant was strongly affected by wind and suggest that this was probably the main factor which determined the more detailed yield responses.

Whilst the major part of this analysis has been concerned with the effects of wind, the effects of phosphorus and particularly nitrogen were often far greater. The effect of wind on the uptake of these two elements was therefore examined. It was found that phosphorus uptake was not significantly affected by wind and that any differences were very small. In the case of nitrogen uptake, the differences were of a similar magnitude but, because of the low variability of this parameter, the effect of wind was significant at 1.0% and the W x N interaction at 2.5%. This is the one parameter where the original data was appreciably different from the modified data since the modification was due to an error in nitrogen application. If the original data is examined, it can be seen that the effect of wind was reduced to 10% significance and also the W x N interaction lost significance.

9.5 Discussion and conclusion

The results of this experiment show clearly that wind decreased the dry matter production of F. arundinacea but for this effect to be significant, the nutrient availability had to be sufficient to ensure good growth of the plants; where phosphorus or nitrogen were limiting, the wind effect became relatively minor.

Many of the parameters showing reductions due to wind were those dependent on the production of new tillers. This was clearly a key aspect. The components of the tillers, for example leaf length, were

were also reduced by wind but to a lesser extent. This could partly have been due to an increased frequency of transverse fold lines, a reflection of leaf damage; occasionally beyond the fold lines there was chlorosis, necrosis or even loss of tissue altogether.

The effects of nitrogen were the most pronounced of the 3 variables and frequently showed an opposite trend to wind. One particularly interesting aspect was the higher nitrogen content of the W_2 plants. This suggests that the depressing effect of wind was potentially more than was apparent as, associated with the higher nitrogen content, the W_2 plants would have been expected to have had higher yields. This may partly explain the lack of significance of the root:shoot ratio results. It would have been interesting to have compared the nitrogen content of the plants used by Whitehead to see if a similar effect occurred in the cases where he reported an increase in the root:shoot ratio.

To some extent, this experiment was exploratory; it was the first time that the controlled environment wind tunnel had been used for a long-term experiment and its reliability was unpredictable. Having established that such experiments were feasible, it was then decided to make the air flow more realistic of natural conditions by introducing turbulence, and then, by using similar experimental conditions, to assess whether yield reductions would also result.

CHAPTER 10.

WIND TUNNEL YIELD EXPERIMENT 2.

10.1 Introduction

The first wind tunnel yield experiment was carried out under conditions where turbulence was created only by the growing crop, the artificial crop and its leading edge. This was reflected in the relatively small amount of leaf flutter observed in the crop when growing in the wind tunnel. This experiment was intended to be more realistic of field conditions by using higher levels of turbulence. The use of cylinders was shown in Chapter 6 to be an effective way of creating turbulence and a cross-piece of cylinders was therefore placed up stream of the working section.

Apart from the higher turbulence, it was intended that all other experimental details should be identical with the procedure used in the first wind tunnel yield experiment.

10.2 Experimental procedure

As one consequence of the introduction of cylinders into the air stream was a disturbance of the pattern of spacial velocity, it was found that conditions identical to those used in the first wind tunnel yield experiment were impossible to achieve. The measurement of the wind speed across the floor of the working section using 9 positions has been described in Chapter 8. This procedure was repeated and changes in spatial velocity were clearly apparent. The setting on the wind tunnel was adjusted until the velocity, averaged over the 9 positions was the same as in the previous experiment; i.e. 3.5m s^{-1}. The velocity produced by the centrifugal fan operating alone was not checked as there was no means by which this could be varied. To achieve the

required velocity across the floor of the tunnel, the unhindered velocity of airflow would have been 11-12m s^{-1}. It should be pointed out that the turbulence patterns in Chapter 6 were obtained by using an unhindered velocity of 7m s^{-1}.

The nutrient conditions used were also different due to the mistaken use of an additional source of slow release nitrogen in the form of hoof and horn. This was added at the rate of 1500 g /1000l as recommended in the U.C. Manual. Also, during the early development stages in the greenhouse, the plants growing in the lower P_1 conditions soon showed slower growth. The phosphorus level was then augmented to 10 p.p.m. by the addition of a further 5 p.p.m. in the form of di-sodium hydrogen orthophosphate. Nevertheless, by the start of the period in the wind tunnel, all plants with the higher level of phosphorus showed greater growth.

The same procedure as in the previous experiment was used in the early stages of development. The plants were allowed to grow in the greenhouse until they had reached a suitable size when they were then transferred to a growth chamber for hardening off before placing in the wind tunnel. The seeds were sown on 9.4.1971 in 2 shallow trays containing a 75% peat:25% fine sand mixture with no added nutrients. After 2 weeks, the seedlings were transplanted into boxes and then left to grow in the greenhouse. Growth was more rapid than in the first experiment due to the more favourable conditions at that time of year.

Because of the difficulties experienced in the previous experiment with periodical de-icing of the growth chamber, a controlled temperature room with greater cooling capacity was modified for wind tunnel use. Two banks of fluorescent tubes were installed, which were spectrally and spatially copies of those in the wind tunnel. It was envisaged that eventually this system might be used as a control for wind tunnel

experiments. At the beginning of each of the experiments in this series, the room was used for adapting the plants to wind tunnel conditions. When experiments were in progress, it was used for housing the plants during the dark period.

On 27.5.1971, 5 weeks after transplanting, the boxes were transferred to the growth room, which was maintained at 10°C with a 12-hour day from 06.00 to 18.00. On 3.6.1971, the temperature setting was lowered to 5°C to harden off the plants and maintained at this level until 16.6.1971 when the experiment started. Unfortunately, at this setting, it was found that the heat generated by the fluorescent tubes was in excess of the capacity of the cooling unit so that during the light periods the temperature gradually rose to 11°C. On 15.6.1971, the numbers of tillers of the central 8 plants in each box was counted and the supplementary amounts of nutrients added. In the first wind tunnel yield experiment, it had been noticed that some of the plants with the high nitrogen application showed some subsequent necrosis of the leaf tips. This was probably due to 600 p.p.m. being an excessive quantity to add on a single occasion. Because of this, only 300 p.p.m. were added at first, the remainder being added 2 weeks later.

The settings on the wind tunnel were 5.5 ± 0.5°C and 80 ± 2% relative humidity. When the plants were stored in the dark, the growth room operated at 4.0 ± 0.5°C.

Three weeks after the start of the previous experiment, the floor of the working section was lowered to account for the increase in plant height but with further increases this was found to be impracticable. In this experiment, this approach was abandoned and the lift mechanism for the box supporting the plants allowed to stop automatically.

The control of temperature in the wind tunnel as described in Chapter 6 operates from a sensor projecting downwards from a central

point approximately 0.5m down wind of the working section. During this experiment, little attempt was made to check on spatial temperature variation in the wind tunnel partly because it was felt that during yield experiments, where temperature might be critical, disturbance of the environmental conditions might spuriously affect the yield results. Such checks were made during a later experiment where yield differences were not important. Had such checks been carried out during this experiment, it would have been realised that, due to a gap of about 1 cm between the rim of the box supporting the plants and the walls of the working section, ambient air was being drawn into the working section. This gap was due to the premature activation of the brake mechanism on the automatic lift system. This could have been over-ridden manually, but it was considered that by leaving such a gap any depletion of the CO_2 in the wind tunnel by the crop would be minimized. Detailed measurements on the effect of this gap were eventually made, but not until this experiment and wind tunnel yield experiment 3 had been completed. These measurements described later showed that,due to this gap, the actual temperatures experienced by the plants were higher than those experienced by the sensor on the roof of the wind tunnel. Moreover, this effect was only apparent in the W_2 wind treatment. It therefore seems likely that the apparent wind effects in this experiment were confounded by differences in temperature. This being so the full details of the yield measurements are not included.

Tiller counts started on 15.6.1971 and, after the count on 23.6.1971, took place at weekly intervals. After 55 days, the final harvest was started and continued replicate by replicate from 10.8.1971 until 21.8.1971. The average date for the harvest was 15.6.1971.

During the course of the experiment, an infection of Erisyphe graminis developed which, although not scored, appeared to be greater

in the W_2 plants. This could be explained by the work of Hammett and Manners (1973) who, in micro wind tunnel studies, reported increased release of conidia from the pustules at increased wind speeds. By periodic spraying, this infection was contained at a low level.

10.3 Results of the weekly tiller counts

The weekly counts of tillers during this experiment as well as the relative growth rates of the intervals between counting are shown in Figures 10.1, 10.2, 10.3 and 10.4. One difference between this experiment and the previous one was the higher initial number of tillers in the P_2 treatments. This was due to the more rapid growth in the greenhouse and contrasts with the slower growth of the P_1 plants where a deficiency developed. The results show that only in the P_2N_1 treatment was there any marked effect of wind, this being associated with an increase in tiller number. To some extent this may have been a reflection of a higher number of tillers initially, but examination of the relative rates of tiller increase showed that such an effect was likely to have been minor. The analysis of variance in the final harvest shows that the effect of wind was only significant in this treatment.

Thus there are 2 interesting contrasts with the previous experiment, firstly the greater response to wind of the P_2N_1 rather than P_2N_2 treatment and secondly the positive rather than negative nature of this response.

The relative growth rates were rather different from those in the first experiment. The clear crossing over effect previously noticed in all cases, was only apparent in the P_1N_1 and P_2N_1 treatments, but this was confused by the final harvest interval. In the period between 28 and 49 days from the start of the experiment, the growth rates of the wind exposed plants were higher in these treatments and this probably

FIGURE 10.1

WIND TUNNEL YIELD EXPERIMENT 2

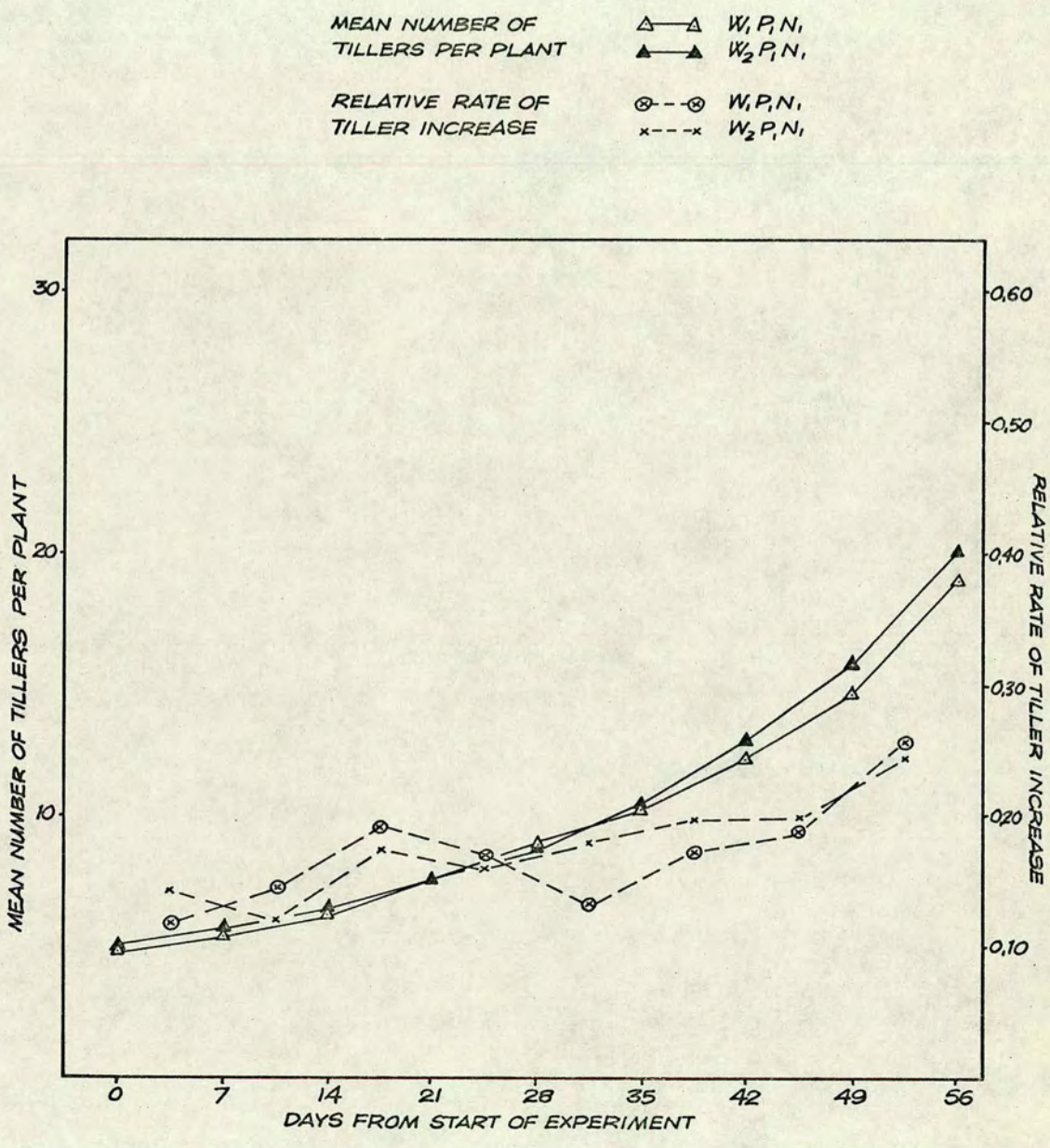


FIGURE 10,2

WIND TUNNEL YIELD EXPERIMENT 2

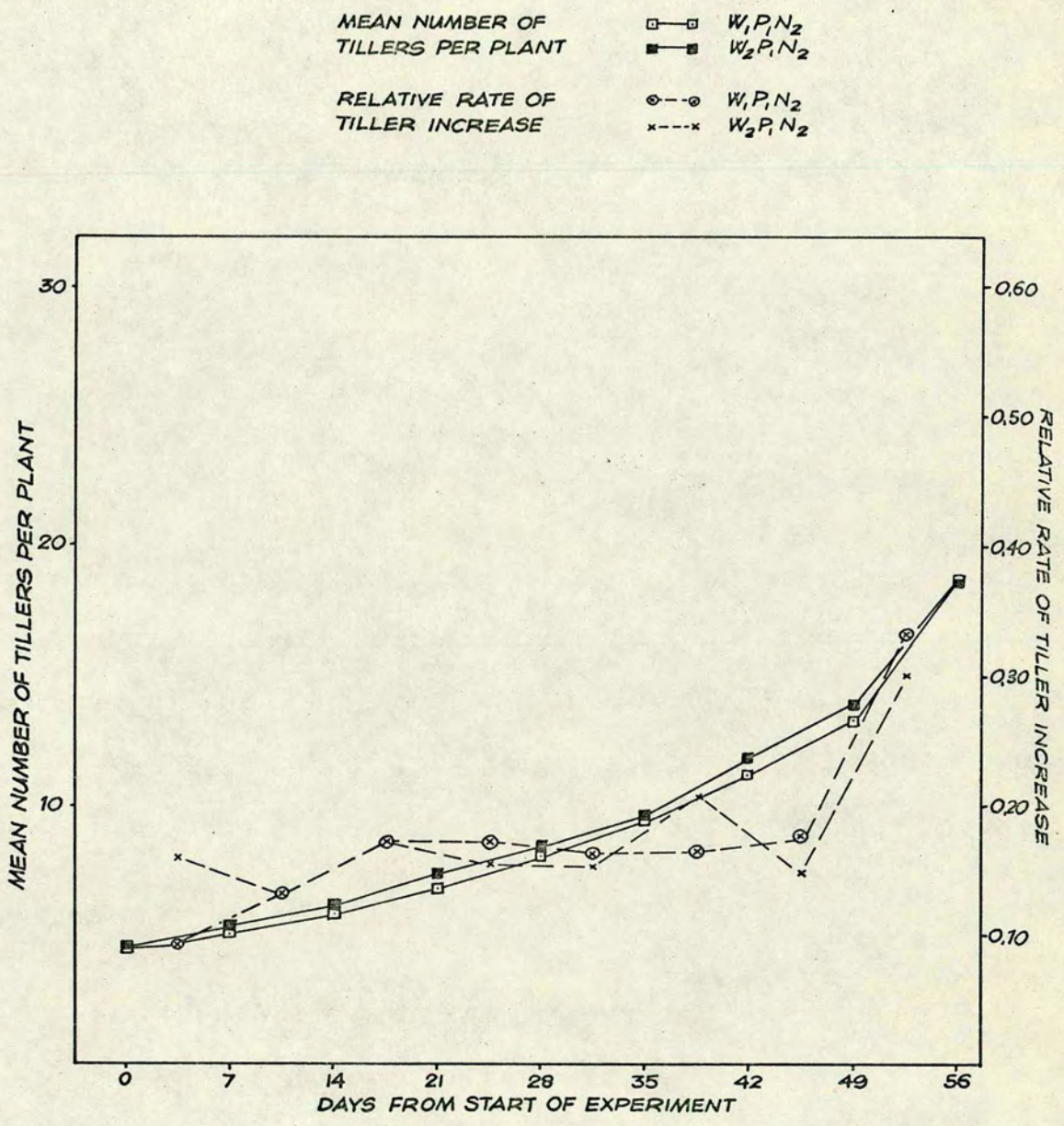


FIGURE 10,3

WIND TUNNEL YIELD EXPERIMENT 2

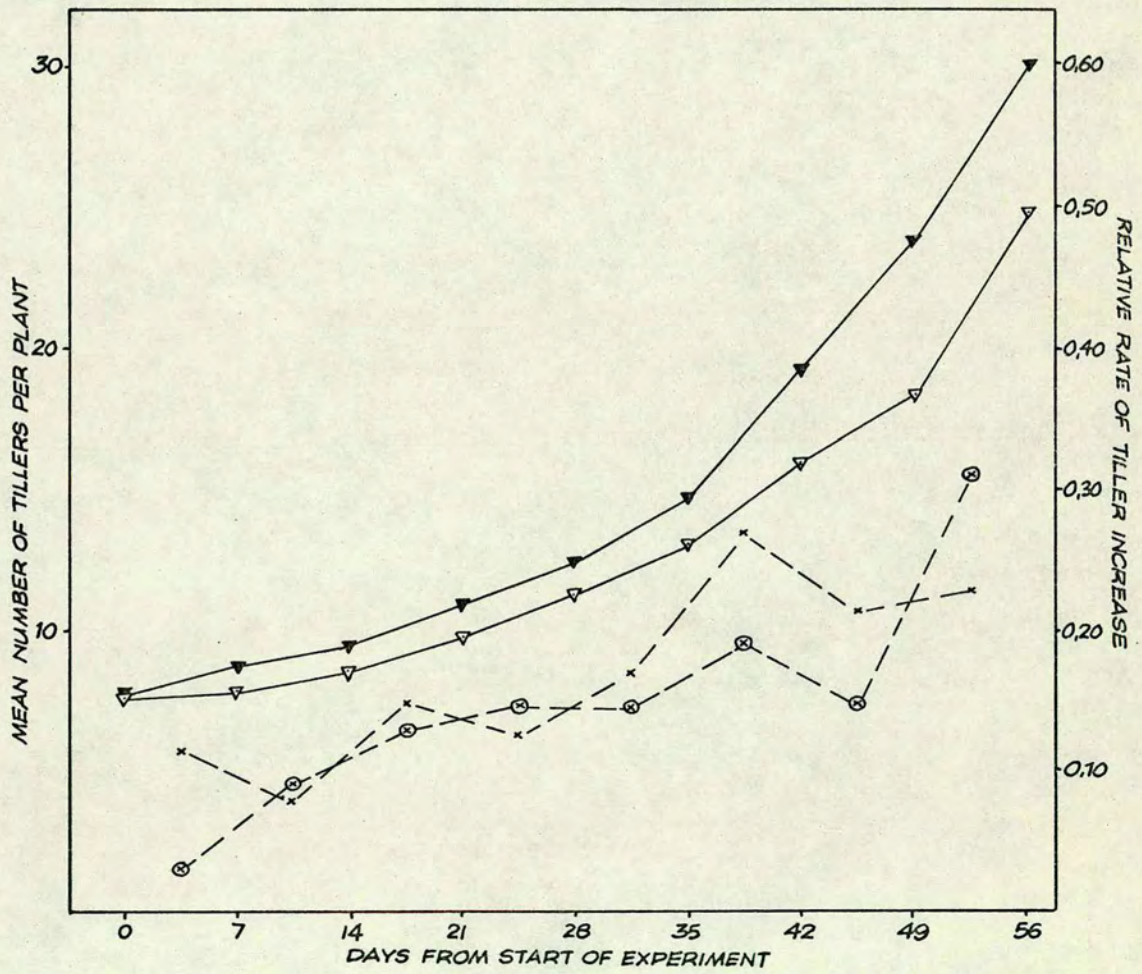
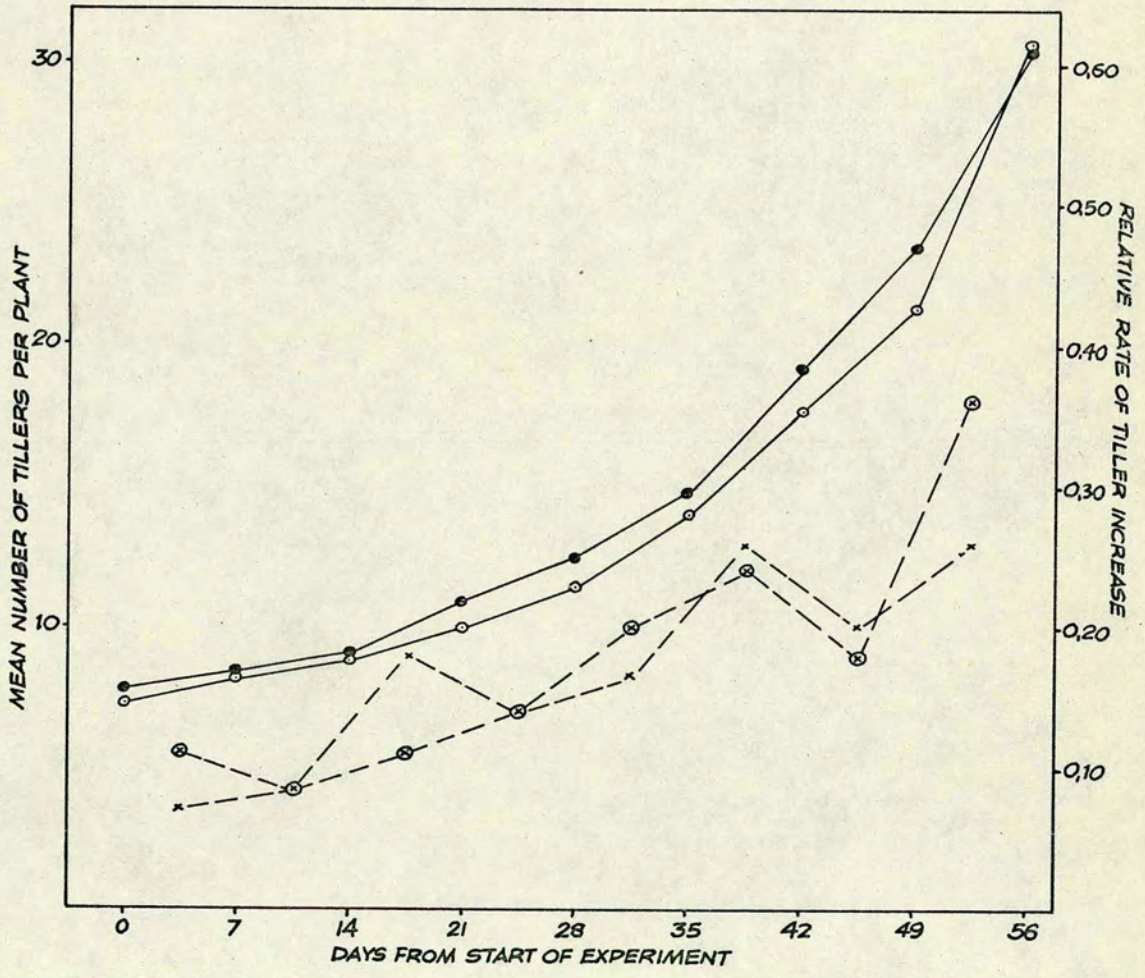


FIGURE 10.4

WIND TUNNEL YIELD EXPERIMENT 2



accounted for the higher tiller numbers attained by the end of the experiment.

10.4 Results of the final harvest

Because of the likelihood of temperature anomalies associated with the W_2 treatments, only a restricted amount of the original data is included in this chapter. This is shown in Tables 10.1, 10.2 and 10.3. Also some of the more interesting parameters are shown in histogram form in Figure 10.5.

Examination of the nitrogen and phosphorus contents of the plants indicated no errors in fertilizer application and so the difficulties concerning the possible use of missing plot techniques experienced previously did not arise in this experiment.

Considering the total dry matter production per plant, there was an overall increase of 0.81% due to wind, an effect which was not significant. The greatest increase in production occurred in the P_2N_1 treatment, but then only of 6.27%. The factor having the most pronounced effect overall was phosphorus which was significant at 0.1% and increased production by 61.46%. By contrast, nitrogen caused an increase of 1.84%, but was not significant.

The dry matter production of shoots was also not significantly affected by wind although the $W_2P_2N_1$ treatment showed an increase of 14.00% above the $W_1P_2N_1$ treatment. Phosphorus was again significant at 0.1% and nitrogen at 1%. The positive effect of wind in these two important parameters was a reversal of the situation in the previous experiment.

The dry weight of roots was just significantly reduced overall by wind (10%), a consistent effect which, in the case of the P_2N_1 treatment, amounted to 13.48%. However, taking an L.S.D. value at 5%, this treat-

WIND TUNNEL YIELD EXPERIMENT 2.

Table 10.1 Overall experimental effects : Final harvest.

Component of yield	Variable	Level 1	Level 2	% Change
TOTAL DRY WEIGHT PER PLANT (mg)	W	983	991	+ 0.81
	P	755	1219	+ 61.46
	N	978	996	+ 1.84
DRY WEIGHT OF SHOOTS PER PLANT (mg)	W	755	784	+ 3.84
	P	568	971	+ 70.95
	N	720	819	+ 13.75
DRY WEIGHT OF ROOTS PER PLANT (mg)	W	228	207	- 9.21
	P	188	248	+ 31.91
	N	258	177	- 31.40
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	W	46.6	57.9	+ 24.25
	P	37.9	66.6	+ 75.73
	N	61.3	43.2	- 29.53
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	W	357	389	+ 8.96
	P	277	468	+ 68.95
	N	331	414	+ 25.08
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	W	351	337	- 3.99
	P	253	436	+ 72.33
	N	328	361	+ 10.06
ROOT : SHOOT RATIO	W	0.34	0.30	- 10.85
	P	0.36	0.29	- 19.33
	N	0.40	0.24	- 39.00
TOTAL LEAF LENGTH PER PLANT (mm)	W	2816	3613	+ 28.30
	P	2503	3927	+ 56.89
	N	2954	3475	+ 17.64

Table 10.1 Overall experimental effects : Final harvest (continued).

Component of yield	Variable	Level 1	Level 2	% Change
NUMBER OF LIVE LEAVES PER PLANT	W	42.17	47.28	+ 12.12
	P	34.96	54.49	+ 55.86
	N	41.76	47.69	+ 14.20
INDIVIDUAL LEAF LENGTH (mm)	W	69	73	+ 5.80
	P	69	73	+ 5.80
	N	68	74	+ 8.82
NUMBER OF DEAD LEAVES PER PLANT	W	6.88	8.49	+ 23.40
	P	6.16	9.22	+ 49.68
	N	9.16	6.22	- 32.10
NUMBER OF TILLERS PER PLANT	W	23.30	24.78	+ 6.35
	P	19.08	29.00	+ 51.99
	N	23.51	24.56	+ 4.47
TOTAL LEAF LENGTH PER TILLER (mm)	W	122	141	+ 15.57
	P	127	136	+ 7.09
	N	121	142	+ 17.36
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	W	1.43	1.43	+ 0.35
	P	1.40	1.47	+ 5.16
	N	1.24	1.62	+ 30.89
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	W	0.41	0.40	- 0.49
	P	0.24	0.57	+139.50
	N	0.40	0.41	+ 2.00
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	W	3.51	3.53	+ 0.46
	P	3.48	3.56	+ 2.07
	N	2.96	4.08	+ 37.93

WIND TUNNEL YIELD EXPERIMENT 2.

Table 10.2 The effect of exposure to wind on yields : Final harvest.

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
TOTAL DRY WEIGHT PER PLANT (mg)	P_1N_1	790	785	- 0.63	-	-
	P_1N_2	725	721	- 0.55		
	P_2N_1	1133	1204	+ 6.27		
	P_2N_2	1283	1254	- 2.26		
DRY WEIGHT OF SHOOTS PER PLANT (mg)	P_1N_1	566	572	+ 1.06	-	-
	P_1N_2	563	569	+ 1.07		
	P_2N_1	814	928	+ 14.00		
	P_2N_2	1075	1066	- 0.84		
DRY WEIGHT OF ROOTS PER PLANT (mg)	P_1N_1	224	212	- 5.36	+	46 mg
	P_1N_2	161	152	- 5.59		
	P_2N_1	319	276	- 13.48		
	P_2N_2	208	187	- 10.10		
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	P_1N_1	37.4	52.6	+ 40.64	+	16 mg
	P_1N_2	26.3	35.5	+ 34.98		
	P_2N_1	71.7	83.6	+ 16.60		
	P_2N_2	51.0	60.0	+ 17.65		
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	P_1N_1	269	273	+ 1.49	+	73 mg
	P_1N_2	277	290	+ 4.69		
	P_2N_1	346	437	+ 26.30		
	P_2N_2	535	554	+ 3.55		
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	P_1N_1	260	247	- 5.00	-	-
	P_1N_2	260	244	- 6.15		
	P_2N_1	396	407	+ 2.78		
	P_2N_2	490	452	- 7.76		

Table 10.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
ROOT : SHOOT RATIO	P_1N_1	0.43	0.41	- 4.65	+	0.06
	P_1N_2	0.30	0.29	- 3.33		
	P_2N_1	0.43	0.33	- 23.26		
	P_2N_2	0.20	0.19	- 5.00		
TOTAL LEAF LENGTH PER PLANT (mm)	P_1N_1	2308	2464	+ 6.76	+	847 mm
	P_1N_2	2556	2683	+ 4.97		
	P_2N_1	2881	4165	+ 44.57		
	P_2N_2	3519	5143	+ 46.15		
NUMBER OF LIVE LEAVES PER PLANT	P_1N_1	33.40	35.95	+ 7.63	+	6.37
	P_1N_2	34.58	35.93	+ 3.90		
	P_2N_1	41.93	55.75	+ 32.96		
	P_2N_2	58.78	61.50	+ 4.63		
INDIVIDUAL LEAF LENGTH (mm)	P_1N_1	66	66	0.00	+	7 mm
	P_1N_2	69	74	+ 7.25		
	P_2N_1	68	73	+ 7.35		
	P_2N_2	72	81	+ 12.50		
NUMBER OF DEAD LEAVES PER PLANT	P_1N_1	6.35	8.25	+ 29.92	+	1.98
	P_1N_2	4.45	5.58	+ 25.39		
	P_2N_1	9.93	12.10	+ 21.85		
	P_2N_2	6.80	8.05	+ 18.38		
NUMBER OF TILLERS PER PLANT	P_1N_1	18.98	20.13	+ 6.06	+	2.93
	P_1N_2	18.63	18.58	- 0.27		
	P_2N_1	24.93	30.03	+ 20.46		
	P_2N_2	30.68	30.38	- 0.98		
TOTAL LEAF LENGTH PER TILLER (mm)	P_1N_1	115	121	+ 5.22	+	20 mm
	P_1N_2	129	143	+ 10.85		
	P_2N_1	111	137	+ 23.42		
	P_2N_2	134	164	+ 22.39		

Table 10.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
RATIO OF NUMBER OF FLAT LEAVES TO NUMBER OF ROUND LEAVES	P_1N_1	1.19	1.27	+ 6.84	-	
	P_1N_2	1.61	1.52	- 5.16		
	P_2N_1	1.31	1.20	- 8.62		
	P_2N_2	1.61	1.75	+ 8.50		
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	P_1N_1	0.22	0.22	+ 2.75	-	
	P_1N_2	0.25	0.26	+ 1.18		
	P_2N_1	0.59	0.57	- 3.73		
	P_2N_2	0.56	0.56	+ 0.72		
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	P_1N_1	3.16	3.18	+ 0.63	-	
	P_1N_2	3.77	3.82	+ 1.33		
	P_2N_1	2.67	2.82	+ 5.62		
	P_2N_2	4.45	4.28	- 3.82		

WIND TUNNEL YIELD EXPERIMENT 2.

Table 10.3 Summary of analyses of variance : Final harvest.

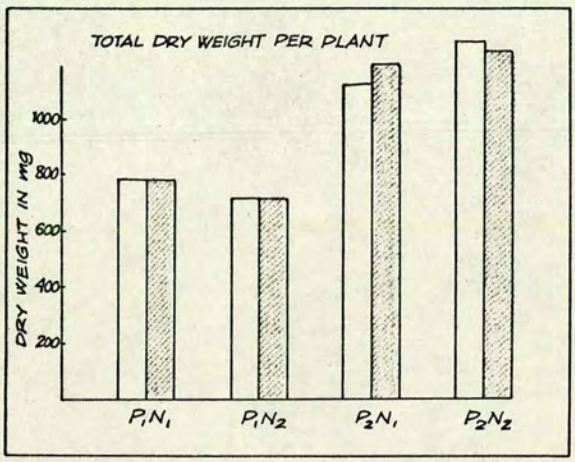
Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
TOTAL DRY WEIGHT PER PLANT	F	0.04	120.05	0.17	0.09	0.33	3.76	0.37
	S	N.S.	0.1	N.S.	N.S.	N.S.	10.0	N.S.
DRY WEIGHT OF SHOOTS PER PLANT	F	0.74	140.98	8.38	0.46	0.83	8.87	0.81
	S	N.S.	0.1	1.0	N.S.	N.S.	1.0	N.S.
DRY WEIGHT OF ROOTS PER PLANT	F	3.60	28.99	52.66	0.90	0.35	2.97	0.19
	S	10.0	0.1	0.1	N.S.	N.S.	10.0	N.S.
DRY WEIGHT OF DEAD LEAVES PER PLANT	F	8.79	56.33	22.64	0.05	0.35	1.12	0.04
	S	1.0	0.1	0.1	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT OF LIVE LEAVES PER PLANT	F	3.19	113.81	21.30	1.68	0.80	15.29	1.26
	S	10.0	0.1	0.1	N.S.	N.S.	0.1	N.S.
DRY WEIGHT OF LEAF SHEATH AND STEM PER PLANT	F	0.54	92.35	3.15	0.00	0.45	3.40	0.35
	S	N.S.	0.1	10.0	N.S.	N.S.	10.0	N.S.
ROOT : SHOOT RATIO	F	5.90	21.95	109.58	2.25	2.04	4.30	2.35
	S	2.5	0.1	0.1	N.S.	N.S.	5.0	N.S.
TOTAL LEAF LENGTH PER PLANT	F	14.78	47.12	6.31	10.02	0.14	1.92	0.20
	S	0.1	0.1	2.5	0.5	N.S.	N.S.	N.S.
NUMBER OF LIVE LEAVES PER PLANT	F	10.75	156.84	14.50	4.12	3.89	11.83	2.52
	S	0.5	0.1	0.1	10.0	10.0	0.5	N.S.
INDIVIDUAL LEAF LENGTH	F	8.49	8.13	14.23	2.26	2.08	0.02	0.00
	S	1.0	1.0	0.1	N.S.	N.S.	N.S.	N.S.

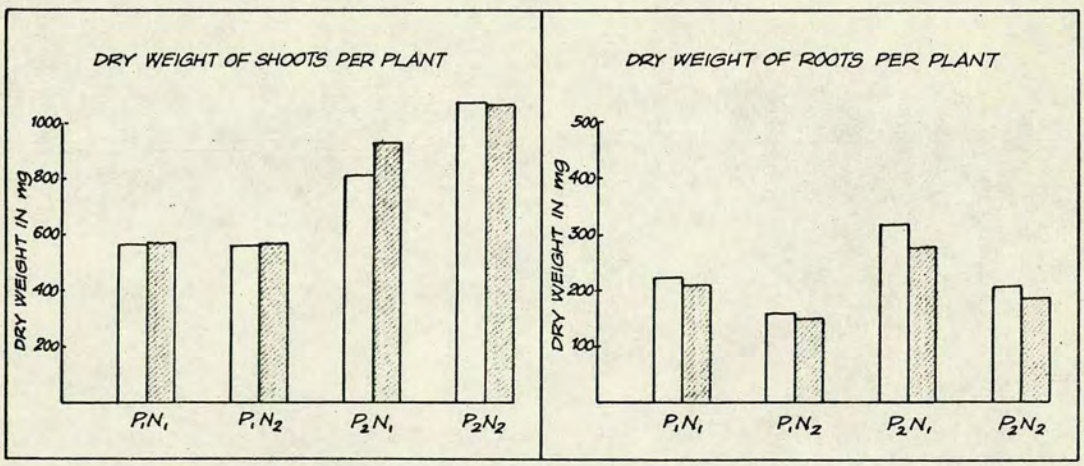
Table 10.3 Summary of analyses of variance : Final harvest (continued).

Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
NUMBER OF DEAD LEAVES PER PLANT	F	11.12	40.10	36.89	0.04	0.77	1.81	0.01
	S	0.5	0.1	0.1	N.S.	N.S.	N.S.	N.S.
NUMBER OF TILLERS PER PLANT	F	4.24	192.06	2.15	1.67	5.31	7.80	2.15
	S	5.0	0.1	N.S.	N.S.	5.0	1.0	N.S.
TOTAL LEAF LENGTH PER TILLER	F	14.70	3.71	19.38	3.26	0.45	0.45	0.03
	S	0.1	10.0	0.1	10.0	N.S.	N.S.	N.S.
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	F	0.00	0.36	10.14	0.00	0.03	0.13	0.74
	S	N.S.	N.S.	0.5	N.S.	N.S.	N.S.	N.S.
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	F	0.09	1866.51	1.12	0.73	0.58	12.02	0.95
	S	N.S.	0.1	N.S.	N.S.	N.S.	0.5	N.S.
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	F	0.07	1.55	369.93	0.11	1.49	72.40	2.22
	S	N.S.	N.S.	0.1	N.S.	N.S.	0.1	N.S.

F : F ratio.
S : Level of significance (%).
N.S. : No significance (for levels greater than 10%).

FIGURE 10.5 WIND TUNNEL YIELD EXPERIMENT 2





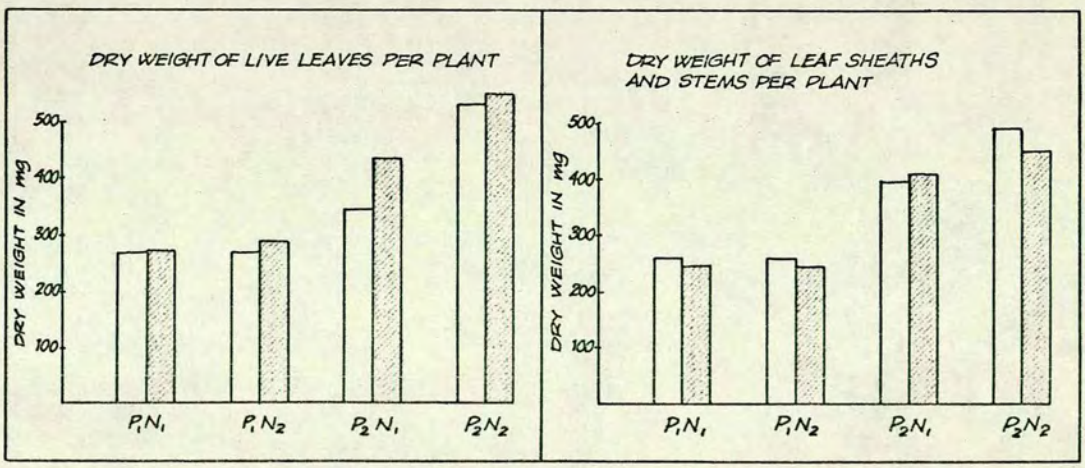
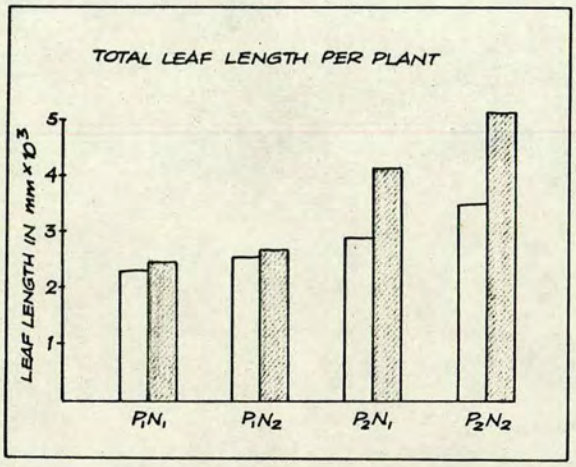
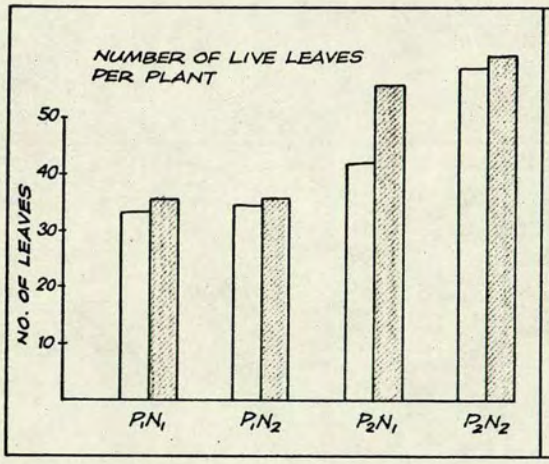
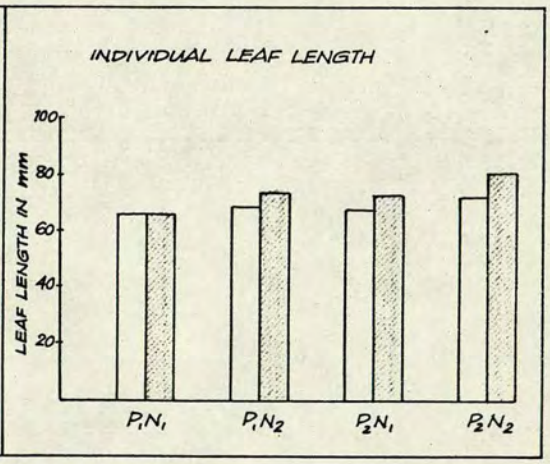
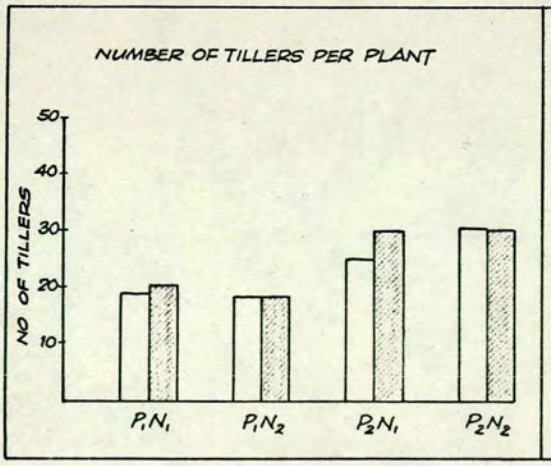


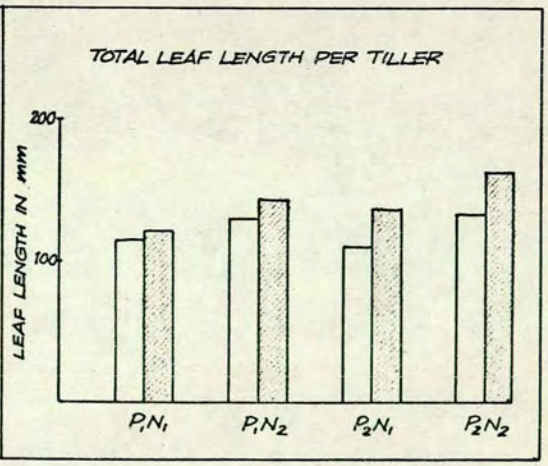
FIGURE 10,5 (CONTINUED) WIND TUNNEL YIELD EXPERIMENT 2











ment difference, although the largest, was not significant. This result was similar to that obtained in the previous experiment, but nitrogen and especially phosphorus had much more pronounced effects and both were significant at 0.1%. Nitrogen, as before, decreased the production of roots whilst phosphorus had the reverse effect.

More detailed examination of the components of the shoots shows that wind increased the dry weight of dead leaves per plant, an effect significant at 1%. The L.S.D. value meant that only the P_1N_1 treatment difference was significant, a treatment not previously having shown any significant effect of wind. This difference amounted to 40.64% and although numerically large, is probably of little meaning biologically.

The dry weight of live leaves per plant was increased by exposure to wind, although this effect was only significant at the 10% level. Examination of the L.S.D. values shows that this applied only to the P_2N_1 treatment where there was an increase of 26.30% due to wind. Both nitrogen and phosphorus increased this parameter and each factor was significant at 0.1% overall.

The dry weight of leaf sheaths and stems was not significantly affected by wind exposure and in none of the treatments did the difference exceed 5%.

The reduction in the dry weight of roots and the generally positive, but not significant, effect of wind on the production of shoots would suggest that the root:shoot ratio would be reduced by wind. An overall effect of wind significant at 2.5% confirmed this hypothesis, but the L.S.D. values showed that this only applied in the P_2N_1 treatment, where it amounted to a reduction of 23.26%. Phosphorus and nitrogen also significantly reduced this parameter.

The total length of leaf per plant was significantly increased by higher levels of wind, phosphorus and nitrogen. Also, there was a

significant W x P interaction. In the case of wind, this overall effect applied only in the P_1N_2 and P_2N_2 treatments. The result for the P_2N_2 treatment, an increase of 46.15% was in contrast to the 37.57% reduction for the corresponding treatment in the previous experiment.

Wind also increased the number of live leaves per plant, an effect significiant overall at 0.5%. Also, the W x N and W x P interactions were significant at 10%. Again the L.S.D. values showed that the P_2N_1 treatment was the only one to which this applied and, in percentage terms, this amounted to an increase of 32.96%.

The individual leaf length was increased overall by wind, phosphorus and nitrogen. Only in the P_2N_2 treatment, where there was an increase of 12.5%, was the effect of wind significant.

The number of dead leaves per plant, reflecting the corresponding dry weight, was increased by exposure to wind and the overall effect was significant at 0.5%. This applied in the P_1N_1 and P_2N_1 treatments.

The number of tillers per plant was increased at the higher levels of wind, phosphorus and nitrogen, these effects being significant at 5%, 0.1% and not significant respectively. Following the general pattern of this experiment, this effect only applied in the P_2N_1 treatment, where there was an increase of 20.46% due to wind. Interestingly, there was also a W x N interaction significant at 5% which, in terms of percentage changes due to wind, appeared as the very slight reductions of 0.27% in the P_1N_2 treatment and 0.98% in the P_2N_2 treatment.

The total leaf length per tiller was also increased by wind overall, an effect significant at 0.1%. Applying only in the P_2N_1 and P_2N_2 treatments, it amounted to increases of 23.42% and 22.39% respectively.

As in the previous experiment, wind had no significant effect on the ratio of flat leaves to round leaves.

The analyses for phosphorus content showed that the overall levels were higher in the P_1N_1, P_1N_2 and P_2N_1 treatments compared with the previous experiment. In the case of the P_1 treatments, this would almost certainly have been due to the application of 10 p.p.m. di-sodium hydrogen orthophosphate instead of 5 p.p.m. as previously. With the P_2N_1 treatments, it would appear that the high level of nitrogen availability in this experiment increased the uptake of phosphorus. Interestingly, the values for the P_2N_2 treatments were almost identical in both experiments. As in the previous experiment, the uptake of phosphorus was unaffected by wind.

Despite the addition of hoof and horn to the soil mixture, the nitrogen content was actually lower in the P_2N_2 treatments in this experiment than in the previous one but in the P_1N_1 and P_2N_1 treatments, values for nitrogen content were larger by a factor of about 2. In this experiment, there was no significant effect of wind on nitrogen uptake.

10.5 Discussion and conclusion

In this experiment, the two most important features of yield, the total dry weight per plant and the dry weight of shoots per plant, were not significantly affected by exposure to the higher windspeed. Also the effect on the number of tillers was less pronounced and only significant at 5%, but clearer responses were shown by the features associated with the leaves. By contrast to the first experiment, these responses were positive so, at the time, the problem was how to explain an increase in certain aspects of yield apparently due to higher turbulence.

Also in this experiment, because of the higher level of nitrogen, the greatest responses to wind were in the P_2N_1 treatment.

Because of the error in fertilizer application and the more inconclusive nature of the yield results, it was decided to repeat the whole experiment.

CHAPTER 11.

WIND TUNNEL YIELD EXPERIMENT 3.

11.1 Introduction

Due to the inconclusive results of wind tunnel yield experiment 2, it was decided to completely repeat this work using essentially the same conditions. This was further justified by the occasional positive effects of wind which previously occurred, a feature which, at the time, could not easily be explained.

11.2 Experimental procedure

It proved impossible to repeat exactly the same velocity distribution across the floor of the wind tunnel as in the previous experiment, so the same procedure of measuring wind velocity at 9 positions across the tunnel floor was adopted. Again the windspeed velocity was adjusted to average 3.5m s^{-1} at crop height.

The nutrient conditions were altered slightly by the omission of hoof and horn erroneously added in the previous experiment and also by using 10 p.p.m. as the low level of phosphorus. This was to guard against the recurrence of any deficiency developing during the period of growth in the greenhouse.

On 21.8.1971 seeds of S.170 Festuca arundinacea were sown in shallow trays containing a 75% peat:25% sand mixture with no added nutrients. After reaching a suitable size, they were transplanted into boxes on 6.9.1971 and then left to grow in the greenhouse. The positions of the boxes were randomized periodically. On 4.10.1971, the boxes were transferred to the controlled temperature room with a 12-hour day from 06.00 to 18.00 with the temperature maintained at 10°C. On 11.10.1971, the temperature was lowered to 5°C to allow the plants to adjust to wind tunnel conditions. Due to a modification of the temperature control unit, no difficulty was experienced in maintaining the room at this

temperature when the lights were on. During this period the plants were again clipped to a height of 8 cm to simulate a light grazing. On 26.10.1971, nutrients were added as appropriate and the initial tiller count taken. On 27.10.1971, the plants were transferred to the wind tunnel at the start of the experiment. Tiller counts took place at weekly intervals and the experiment was terminated by a destructive harvest as described previously. This lasted from 15.12.1971 to 23.12.1971. Thus the average date for the final harvest was 19.12.1971.

More difficulties than usual were experienced with the temperature and humidity controls of the wind tunnel during this experiment. On 3.11.1971, the humidity control system failed completely and had to be operated manually overnight. On 7.11.1971, further difficulties were experienced with both temperature and humidity controls when the temperature rose to 11^{o}C and the humidity to 98% before correction. This fault was rectified on 9.11.1971. On 13.11.1971, due to problems with the water supply to the building, the temperature rose to 12^{o}C and the humidity to 98% before correction. Further problems with the water supply on 19.11.1971 necessitated turning off the humidity controls for 2 hours. On 20.11.1971, due to a burst pipe in the growth room, a number of boxes were flooded and suffered some loss of soil.

The settings for the wind tunnel were again 5.5 $\pm$ 0.5^{o}C for temperature and 80 $\pm$ 2% for relative humidity. The air temperatures experienced by the plants were probably in excess of this due to warm air being drawn into the working section. Because of this, the results of this experiment must be regarded with suspicion and therefore are not included in very great detail.

11.3 Results of the weekly tiller counts

The results of the weekly tiller counts are shown in Figures 11.1,

FIGURE 11.1

WIND TUNNEL YIELD EXPERIMENT 3

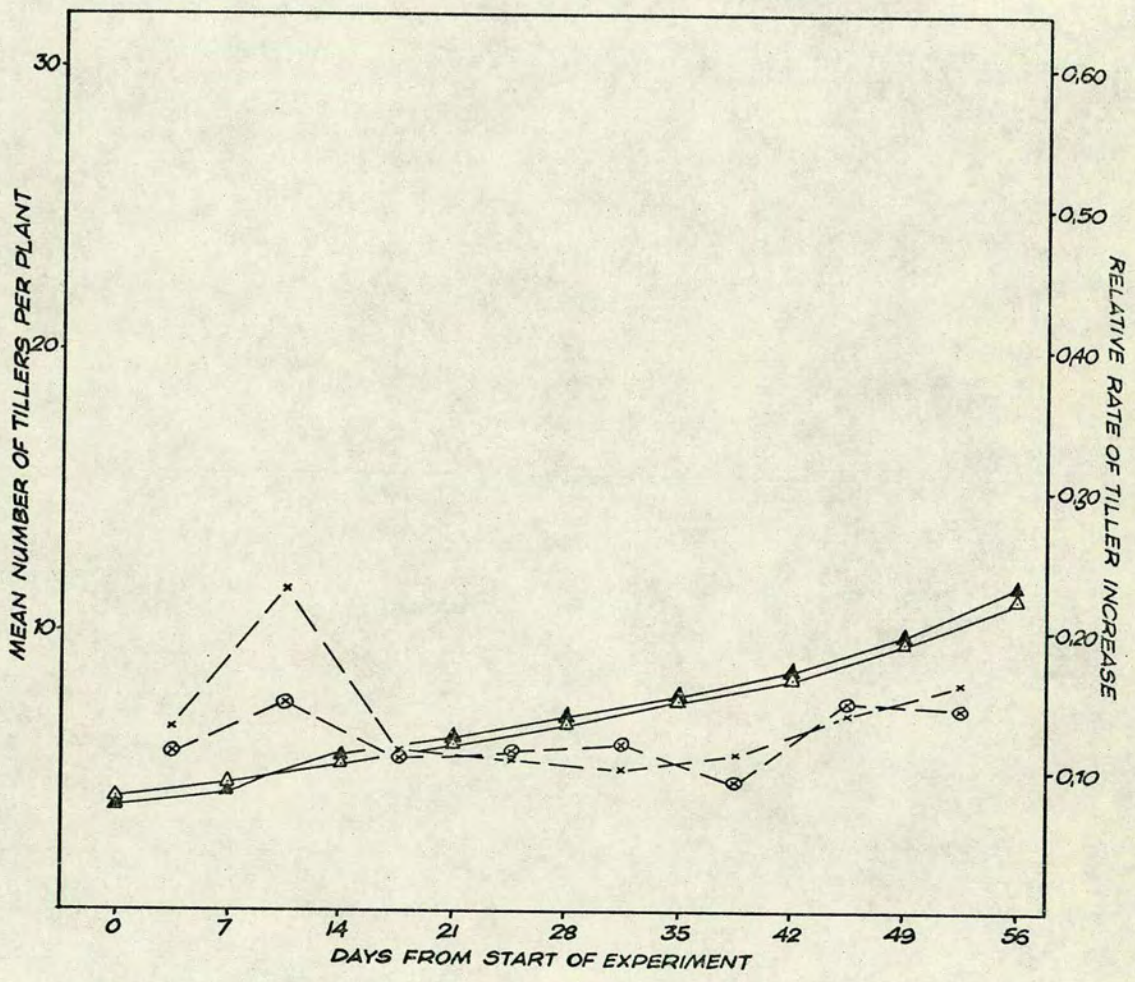


FIGURE 11,2 WIND TUNNEL YIELD EXPERIMENT 3

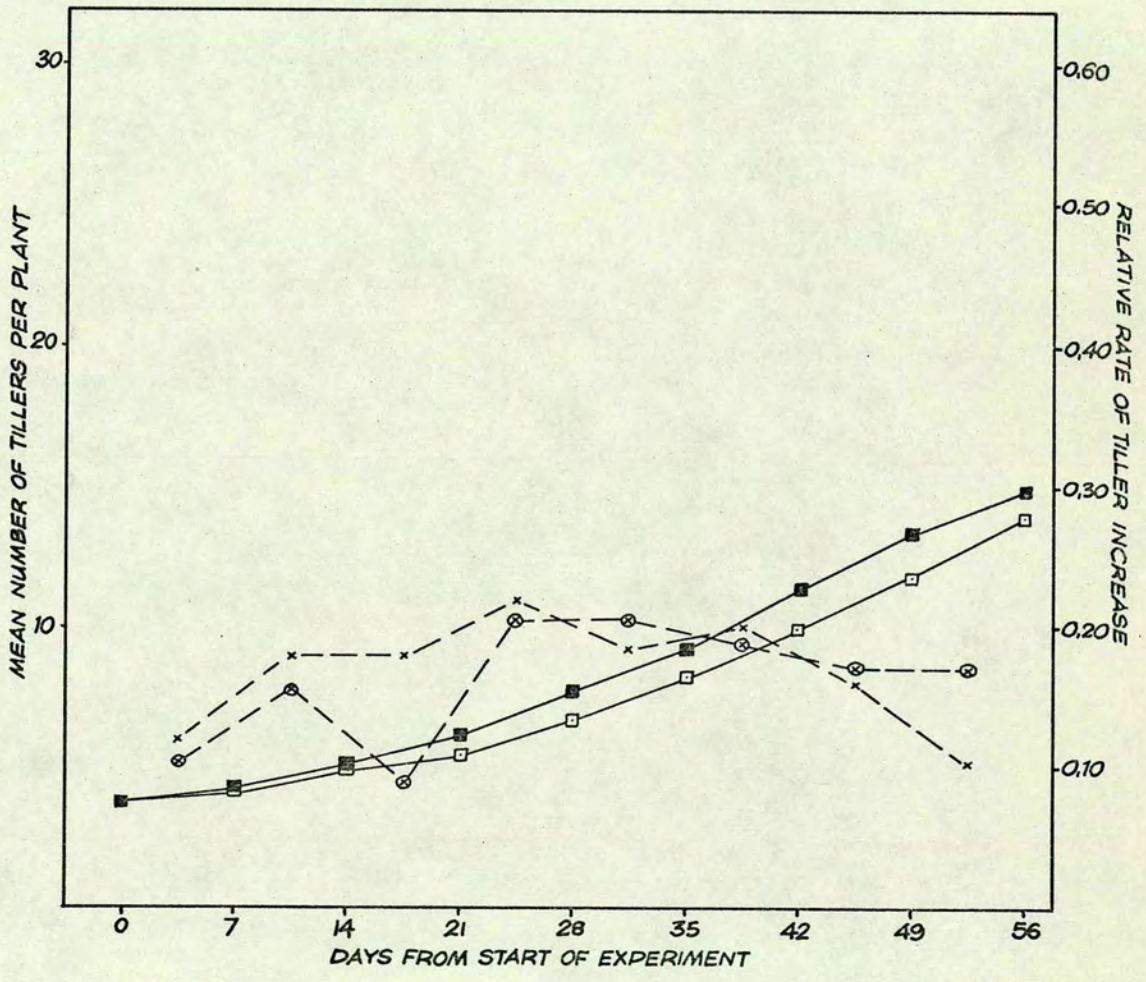


FIGURE 11,3

WIND TUNNEL YIELD EXPERIMENT 3

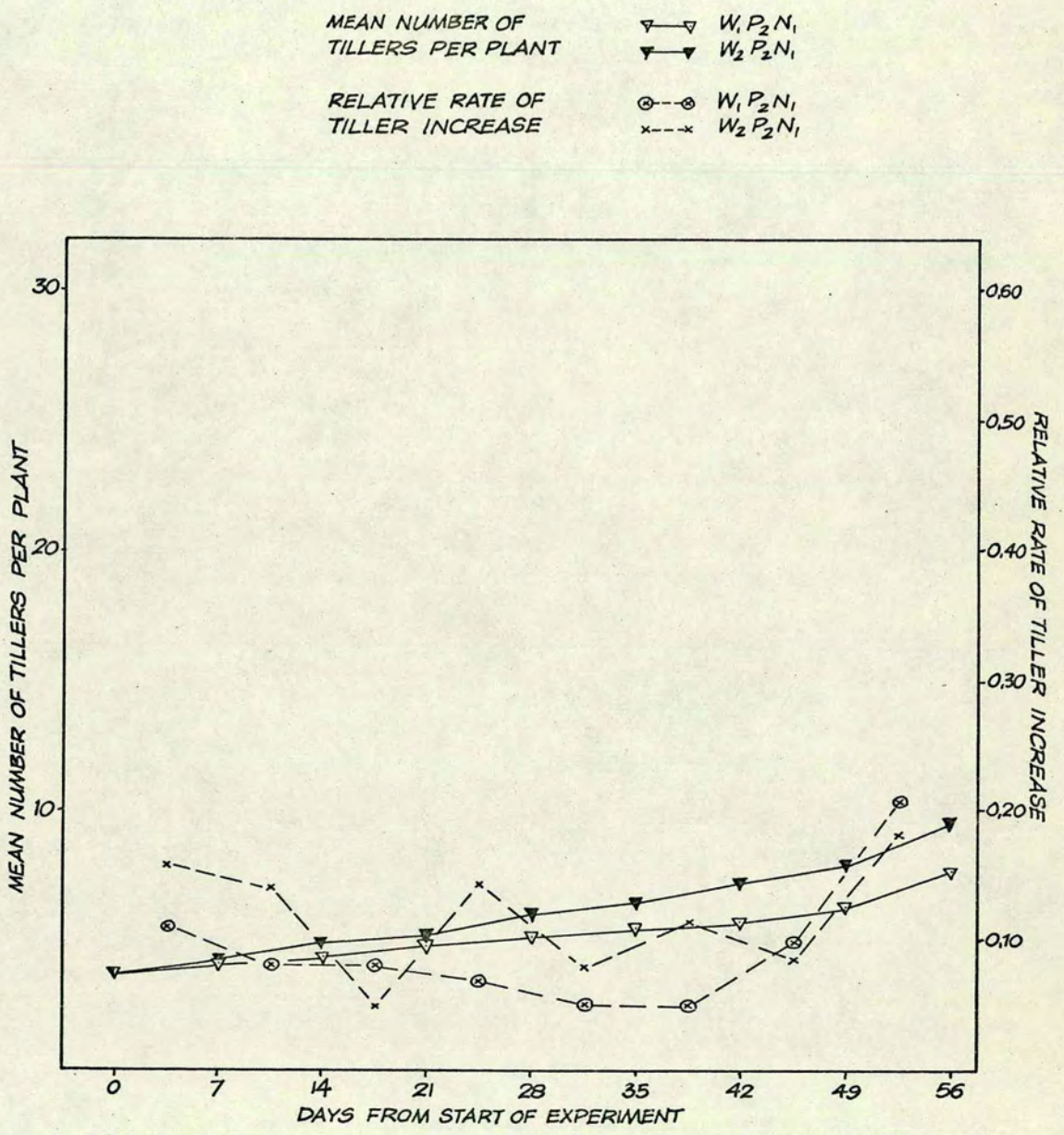
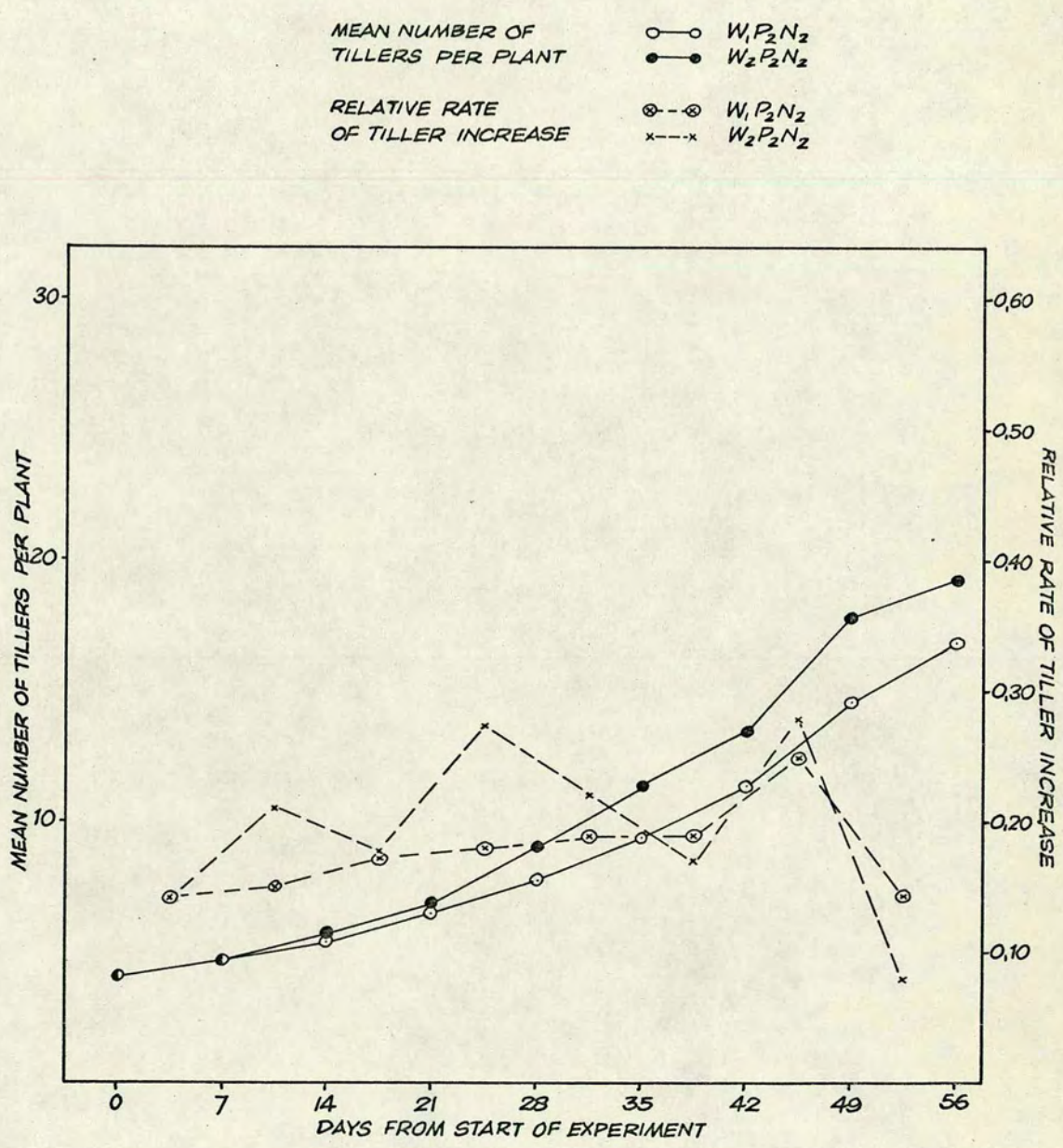


FIGURE 11,4

WIND TUNNEL YIELD EXPERIMENT 3



11.2, 11.3 and 11.4, where each value is the mean of the 5 replicates and thus of 40 plants. At the start of this experiment, the number of tillers per plant was generally less than in wind tunnel yield experiment 2, especially in the P_2N_1 and P_2N_2 treatments. This was due to both the shorter day length and shorter period whilst in the greenhouse, and the exclusion of hoof and horn from the growth medium. The average number was slightly less than 4 compared with about 4.5 for the P_1N_1 and P_1N_2 treatments and about 7.5 for the P_2N_1 and P_2N_2 treatments in the previous experiment.

The results show that, in all cases, the plants exposed to the W_2 windspeed had the greater number of tillers. This was especially so in the P_2N_2 treatment, where this effect definitely arose from a faster growth rate rather than from any possible differences in the initial numbers of tillers which were identical. The effect of wind on the other treatments, especially the P_1N_1 and P_1N_2, was very slight and in the analysis of variance of this parameter in the final harvest, only the P_2N_2 treatment was found to have been significantly affected.

The relative growth rates of the plants exposed to the W_2 windspeed tended to be higher initially, but lower by the final interval between counts in all treatments except P_1N_1. This parameter was rather variable but the pattern which appeared in this experiment seemed similar, though opposite, to that observed in yield experiment 1.

11.4 Results of the final harvest

The results of the final harvest of this experiment are shown in Tables 11.1, 11.2 and 11.3, with some of the more interesting parameters appearing as histograms in Figure 11.5.

In this experiment, the total dry matter production per plant was increased by wind, this effect being significant at 5%. When the L.S.D.

WIND TUNNEL YIELD EXPERIMENT 3.

Table 11.1 Overall experimental effects : Final harvest.

Component of yield	Variable	Level 1	Level 2	% Change
TOTAL DRY WEIGHT PER PLANT (mg)	W	537	595	+ 10.80
	P	574	558	- 2.79
	N	504	628	+ 24.60
DRY WEIGHT OF SHOOTS PER PLANT (mg)	W	383	431	+ 12.53
	P	404	410	+ 1.49
	N	314	500	+ 59.24
DRY WEIGHT OF ROOTS PER PLANT (mg)	W	153	164	+ 7.19
	P	171	147	- 14.04
	N	190	127	- 33.16
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	W	20.3	20.7	+ 1.97
	P	19.6	21.4	+ 9.18
	N	22.8	18.2	- 20.18
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	W	182	217	+ 19.23
	P	194	206	+ 6.19
	N	137	262	+ 91.24
DRY WEIGHT OF LEAF SHEATH AND STEM PER PLANT (mg)	W	181	193	+ 6.63
	P	190	183	- 3.68
	N	154	219	+ 42.21
ROOT : SHOOT RATIO	W	0.47	0.46	- 0.43
	P	0.46	0.47	+ 0.86
	N	0.66	0.27	- 59.03
TOTAL LEAF LENGTH PER PLANT (mm)	W	1552	1914	+ 23.32
	P	1597	1869	+ 17.03
	N	1064	2402	+125.75

Table 11.1 Overall experimental effects : Final harvest (continued).

Component of yield	Variable	Level 1	Level 2	% Change
NUMBER OF LIVE LEAVES PER PLANT	W	23.20	27.64	+ 19.14
	P	24.52	26.33	+ 7.37
	N	17.54	33.30	+ 89.81
INDIVIDUAL LEAF LENGTH (mm)	W	65	68	+ 4.62
	P	66	67	+ 1.52
	N	62	71	+ 14.52
NUMBER OF DEAD LEAVES PER PLANT	W	3.68	3.92	+ 6.47
	P	3.73	3.87	+ 3.70
	N	4.24	3.36	- 20.65
NUMBER OF TILLERS PER PLANT	W	12.44	13.90	+ 11.70
	P	12.94	13.40	+ 3.52
	N	10.04	16.30	+ 62.29
TOTAL LEAF LENGTH PER TILLER (mm)	W	120	131	+ 9.17
	P	124	128	+ 3.23
	N	107	144	+ 34.58
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	W	1.18	1.22	+ 2.79
	P	1.05	1.35	+ 27.85
	N	1.04	1.36	+ 31.59
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	W	0.45	0.43	- 3.98
	P	0.30	0.59	+ 95.33
	N	0.41	0.48	+ 16.63
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	W	3.07	3.06	- 0.49
	P	3.00	3.13	+ 4.47
	N	1.62	4.51	+178.41

WIND TUNNEL YIELD EXPERIMENT 2.

Table 11.2 The effect of exposure to wind on yields : Final harvest.

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
TOTAL DRY WEIGHT PER PLANT (mg)	P_1N_1	581	559	- 3.79	+	109 mg
	P_1N_2	552	605	+ 9.60		
	P_2N_1	417	461	+ 10.55		
	P_2N_2	600	754	+ 25.67		
DRY WEIGHT OF SHOOTS PER PLANT (mg)	P_1N_1	362	357	- 1.38	+	84 mg
	P_1N_2	427	470	+ 10.07		
	P_2N_1	257	281	+ 9.34		
	P_2N_2	486	616	+ 26.75		
DRY WEIGHT OF ROOTS PER PLANT (mg)	P_1N_1	219	202	- 7.76	-	-
	P_1N_2	125	136	+ 8.80		
	P_2N_1	160	180	+ 12.50		
	P_2N_2	110	138	+ 25.45		
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	P_1N_1	20.2	22.6	+ 11.88	-	-
	P_1N_2	19.2	16.5	- 14.06		
	P_2N_1	22.8	25.6	+ 12.28		
	P_2N_2	19.0	18.2	- 4.21		
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	P_1N_1	155	163	+ 5.16	+	46 mg
	P_1N_2	212	245	+ 15.57		
	P_2N_1	110	122	+ 10.91		
	P_2N_2	254	340	+ 33.86		
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	P_1N_1	186	171	- 8.06	-	-
	P_1N_2	196	209	+ 6.63		
	P_2N_1	125	133	+ 6.40		
	P_2N_2	215	258	+ 20.00		

Table 11.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
ROOT : SHOOT RATIO	P_1N_1	0.64	0.61	- 4.69	-	-
	P_1N_2	0.31	0.30	- 3.23		
	P_2N_1	0.68	0.71	+ 4.41		
	P_2N_2	0.24	0.24	0.00		
TOTAL LEAF LENGTH PER PLANT (mm)	P_1N_1	1194	1313	+ 9.97	+	623 mm
	P_1N_2	1838	2043	+ 11.15		
	P_2N_1	778	972	+ 24.94		
	P_2N_2	2398	3328	+ 38.78		
NUMBER OF LIVE LEAVES PER PLANT	P_1N_1	19.48	20.80	+ 6.78	+	6.06
	P_1N_2	27.15	30.65	+ 12.89		
	P_2N_1	13.00	16.90	+ 30.00		
	P_2N_2	33.18	42.23	+ 27.28		
INDIVIDUAL LEAF LENGTH (mm)	P_1N_1	61	65	+ 6.56	-	-
	P_1N_2	69	70	+ 1.45		
	P_2N_1	62	60	+ 3.23		
	P_2N_2	69	76	+ 10.15		
NUMBER OF DEAD LEAVES PER PLANT	P_1N_1	3.80	4.68	+ 23.16	-	-
	P_1N_2	3.58	2.88	- 19.55		
	P_2N_1	3.88	4.60	+ 18.56		
	P_2N_2	3.48	3.53	+ 1.44		
NUMBER OF TILLERS PER PLANT	P_1N_1	11.13	11.75	+ 5.57	+	2.32
	P_1N_2	13.98	14.93	+ 6.80		
	P_2N_1	7.73	9.58	+ 23.93		
	P_2N_2	16.95	19.35	+ 14.16		

Table 11.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
TOTAL LEAF LENGTH PER TILLER (mm)	P_1N_1	105	111	+ 5.71	+	19 mm
	P_1N_2	135	144	+ 6.67		
	P_2N_1	106	108	+ 1.89		
	P_2N_2	136	163	+ 19.85		
RATIO OF NUMBER OF FLAT LEAVES TO NUMBER OF ROUND LEAVES	P_1N_1	0.84	1.02	+ 21.00	-	-
	P_1N_2	1.13	1.21	+ 6.98		
	P_2N_1	1.21	1.07	- 12.27		
	P_2N_2	1.54	1.57	+ 1.76		
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	P_1N_1	0.29	0.28	- 4.11	-	-
	P_1N_2	0.31	0.32	+ 2.59		
	P_2N_1	0.57	0.50	- 13.00		
	P_2N_2	0.64	0.64	+ 0.94		
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%)	P_1N_1	1.83	1.67	- 8.74	-	-
	P_1N_2	4.15	4.36	+ 5.06		
	P_2N_1	1.43	1.56	+ 9.09		
	P_2N_2	4.90	4.65	- 5.10		

WIND TUNNEL YIELD EXPERIMENT 3.

Table 11.3 Summary of analyses of variance : Final harvest.

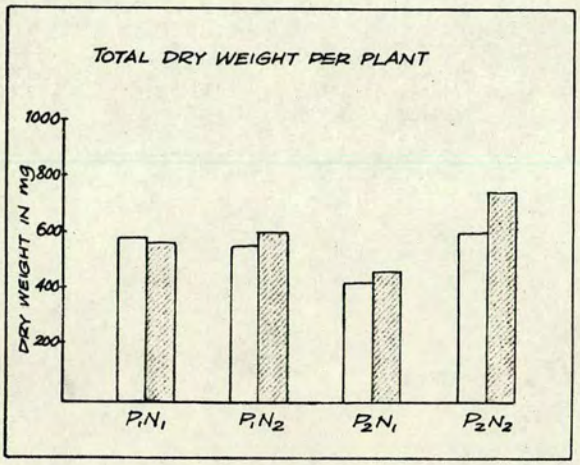
Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
TOTAL DRY WEIGHT PER PLANT	F	4.61	0.37	21.33	2.42	3.03	18.44	0.11
	S	5.0	N.S.	0.1	N.S.	10.0	0.1	N.S.
DRY WEIGHT OF SHOOTS PER PLANT	F	5.45	0.10	82.42	1.98	3.55	22.27	0.51
	S	5.0	N.S.	0.1	N.S.	10.0	0.1	N.S.
DRY WEIGHT OF ROOTS PER PLANT	F	1.60	7.93	56.67	2.70	1.13	4.36	0.36
	S	N.S.	1.0	0.1	N.S.	N.S.	5.0	N.S.
DRY WEIGHT OF DEAD LEAVES PER PLANT	F	0.05	0.73	4.82	0.07	1.09	0.24	0.03
	S	N.S.	N.S.	5.0	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT OF LIVE LEAVES PER PLANT	F	9.36	1.25	121.12	1.65	4.77	24.12	1.12
	S	0.5	N.S.	0.1	N.S.	5.0	0.1	N.S.
DRY WEIGHT OF LEAF SHEATH AND STEM PER PLANT	F	1.66	0.67	48.97	1.97	2.72	20.22	0.03
	S	N.S.	N.S.	0.1	N.S.	N.S.	0.1	N.S.
ROOT : SHOOT RATIO	F	0.02	0.04	502.76	1.00	0.02	15.88	0.97
	S	N.S.	N.S.	0.1	N.S.	N.S.	0.1	N.S.
TOTAL LEAF LENGTH PER PLANT	F	5.63	3.17	76.81	1.72	1.81	18.20	1.14
	S	2.5	10.0	0.1	N.S.	N.S.	0.1	N.S.
NUMBER OF LIVE LEAVES PER PLANT	F	8.96	1.48	112.58	1.87	1.52	22.18	0.25
	S	1.0	N.S.	0.1	N.S.	N.S.	0.1	N.S.

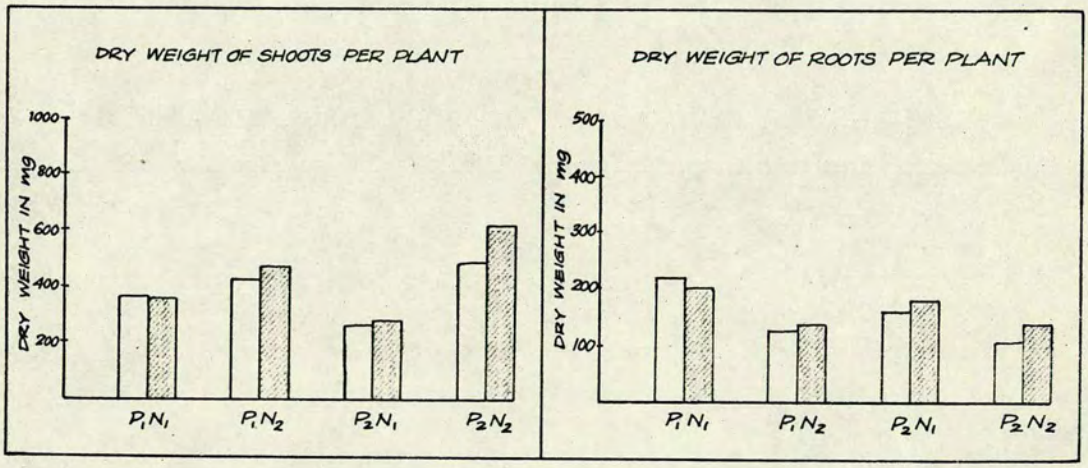
Table 11.3 Summary of analyses of variance : Final harvest (continued).

Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
INDIVIDUAL LEAF LENGTH	F	2.32	0.26	32.58	0.00	1.61	2.72	3.15
	S	N.S.	N.S.	0.1	N.S.	N.S.	N.S.	10.0
NUMBER OF DEAD LEAVES PER PLANT	F	0.82	0.27	11.11	0.33	4.95	0.27	0.73
	S	N.S.	N.S.	0.5	N.S.	5.0	N.S.	N.S.
NUMBER OF TILLERS PER PLANT	F	6.59	0.65	121.63	1.39	0.42	32.70	0.01
	S	2.5	N.S.	0.1	N.S.	N.S.	0.1	N.S.
TOTAL LEAF LENGTH PER TILLER	F	5.71	0.96	64.60	0.58	2.18	1.43	1.64
	S	2.5	N.S.	0.1	N.S.	N.S.	N.S.	N.S.
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	F	0.14	10.92	13.46	1.12	0.05	0.94	0.60
	S	N.S.	0.5	0.1	N.S.	N.S.	N.S.	N.S.
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	F	2.69	700.80	39.04	2.21	5.25	13.74	1.88
	S	N.S.	0.1	0.1	N.S.	5.0	0.1	N.S.
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	F	0.05	3.70	1735.02	0.40	0.00	31.55	7.04
	S	N.S.	10.0	0.1	N.S.	N.S.	0.1	2.5

F : F ratio.
S : Level of significance (%).
N.S. : No significance (for levels greater than 10%).

FIGURE 11.5 WIND TUNNEL YIELD EXPERIMENT 3





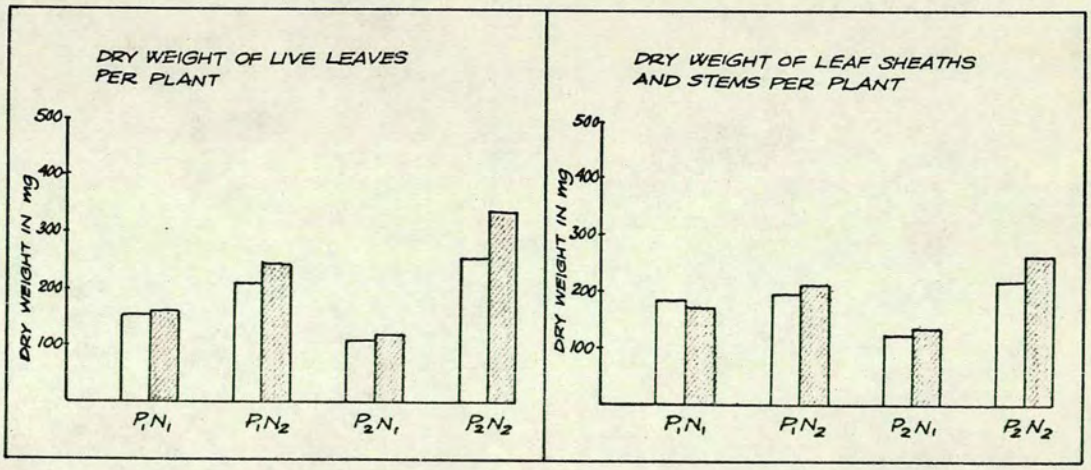
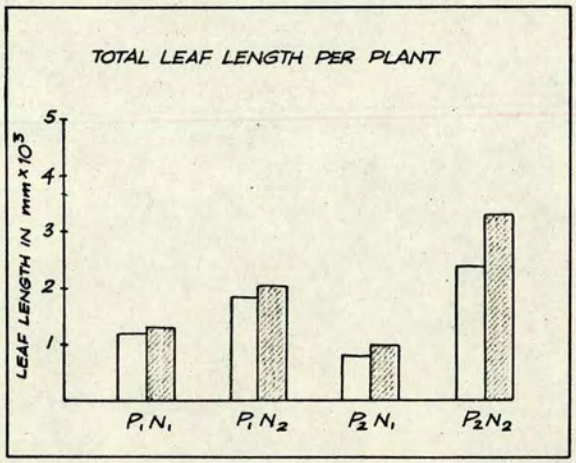
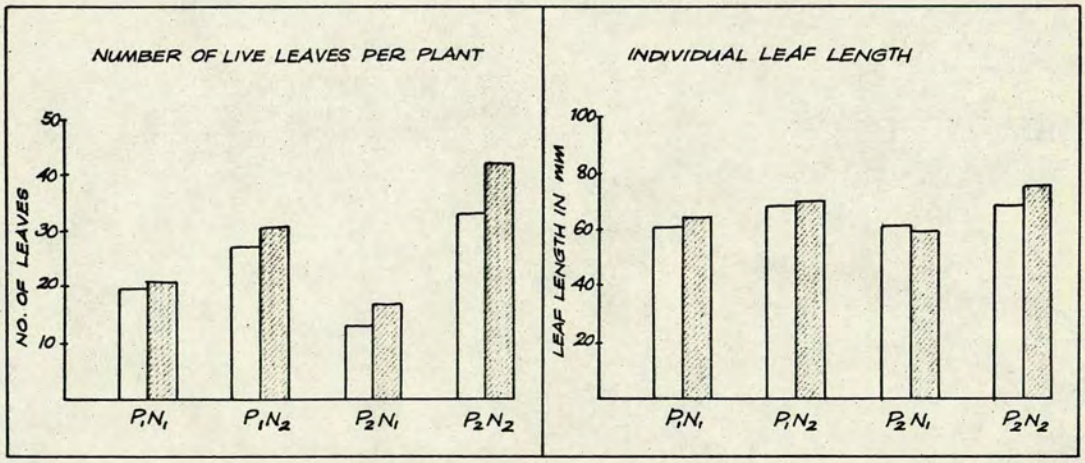
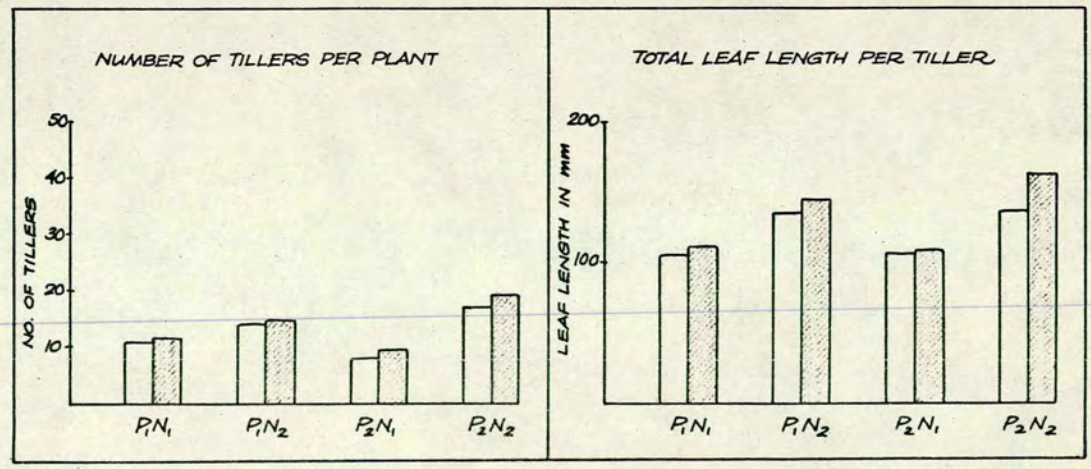


FIGURE 11.5 (CONTINUED) WIND TUNNEL YIELD EXPERIMENT 3







value was examined, it appeared that the only significant difference occurred in the P_2N_2 treatment, where there was a 25.67% increase in yield due to wind. The P_1N_1 treatment actually showed a reduction in yield at the higher windspeed, but only of 3.79% and this not significant. Nevertheless, this was reflected in the W x N interaction, which had overall significance at 10%. The nutrient responses resembled the first yield experiment more than the second, with nitrogen resulting in an overall increase of 24.60%, an effect significant at 0.1%. Phosphorus produced a slight, but not significant, depression in yield. This may have been due to the addition of 10 p.p.m. rather than 5 p.p.m. in the P_1 treatment, thus reducing the contrast between that and the P_2 treatment.

The results for the dry weight of shoots per plant showed a similar pattern. Again, wind had a positive effect overall, which was significant at 5%, although this was specifically confined to the P_2N_2 treatments increasing yield by 26.75%. The P_1N_1 treatments showed a small decrease of 1.38%, which although not significant, was probably a contributory factor in the significance at 10% of the W x N interaction. The effect of nitrogen was again significant overall at 0.1% and produced an increase of 59.24%. Phosphorus produced an increase of only 1.49% and this effect had no overall significance.

The dry weight of roots was not significantly affected overall by exposure to the higher windspeed, even though the P_2N_2 plants so exposed had 25.45% higher dry weights. Phosphorus and nitrogen both decreased this parameter significantly, phosphorus by 14.04% and nitrogen by 33.16% overall.

The dry weight of dead leaves per plant was not significantly affected by wind or phosphorus, but nitrogen caused a 20.18% reduction. However, this effect was very small in absolute terms.

The dry weight of live leaves per plant was, again, a responsive feature and both wind and nitrogen had positive effects. Wind produced a 19.23% increase overall and a 33.86% increase in the P_2N_2 treatment. Nitrogen increased yield by 91.24% and also, the W x N interaction was significant.

The dry weight of leaf sheaths and stems per plant was significantly increased by nitrogen but, even though wind caused a 20.00% increase in the P_2N_2 treatment, the effects of both wind and phosphorus were not significant.

The root:shoot ratio was very little affected by wind either in absolute or percentage terms and such effects as occurred were not significant. Nitrogen had a significant and striking effect causing a 59.03% reduction.

The total leaf length per plant again responded strongly to the experimental variables, all of which had significant positive effects overall. Wind increased length by 23.32%, phosphorus by 17.03% and nitrogen by 125.75%. In the case of wind, only the P_2N_2 treatment was significant where there was a 38.78% increase due to wind.

Reflecting the total leaf length, the number of live leaves per plant also showed a significant and positive effect of wind amounting to 19.14% overall. Phosphorus was not significant but nitrogen increased this parameter by 89.81% overall. In the P_2N_2 treatment, wind caused a 27.28% increase in leaf number, whilst in the P_2N_1 treatment, the increase was 30.00% but here, because of the small absolute values, the effect was not significant.

By contrast to the previous experiment, the individual leaf length was not significantly altered by exposure to the higher windspeed, although in the P_2N_2 treatment there was an increase of 10.15%. Nitrogen

increased the overall length by 14.52%, an effect significant at 0.1%.

The number of dead leaves per plant was not significantly affected by exposure to wind.

The pattern from these results again indicated particularly strong responses to wind in those parameters dependent on the rate of tiller production. Examination of the number of tillers per plant shows that wind caused an overall increase of 11.70%, an effect significant at 2.5%. Again,this only applied to the P_2N_2 treatment, where the increase was 14.16%. The effect of phosphorus was not significant but nitrogen, which was significant at 0.1%, caused 62.29% increase in numbers overall.

Leaf length, so responsive a character when examined on a per plant basis, was also significantly increased by exposure to wind when examined on a per tiller basis. This amounted to 9.17% overall and to 19.85% in the P_2N_2 treatment, the only one that was significant after examination of the L.S.D. values. Phosphorus had no significant effect on this parameter, but nitrogen was significant at 0.1% and caused an overall increase in length of 34.58%.

The ratio of the number of flat leaves to round leaves was again not significantly affected by wind.

The final points of interest in this experiment are the levels of nitrogen and phosphorus in the border plants. These were found to resemble more closely those of the first wind tunnel yield experiment than the second, but there was a higher phosphorus content overall especially in the P_1 treatments, which probably reflected the initial addition of 10 p.p.m. rather than 5 p.p.m. phosphorus. Wind had no significant effect on phosphorus uptake but,interestingly, the W x N interaction was significant at 5%.

The nitrogen levels were also similar to the first wind tunnel yield experiment when hoof and horn was not added. Levels in the P_1N_2

treatments were however higher probably due to the greater availability of phosphorus. Wind had no significant effect on nitrogen uptake but the second order W x P x N interaction was significant at the 2.5% level.

11.5 Discussion and conclusion

Had it not been for the later discovery of the air temperature differences due to the gap in the working section, these results would probably have been accepted as confirmation of the less conclusive results in the second wind tunnel yield experiment. The conclusion would therefore have been that wind, when turbulent, enhances the growth of S.170 *F. arundinacea*, especially under conditions of high nutrient availability. Because such a result would have contrasted so dramatically with that which might have been expected, considerable effort was made to investigate the causes. The details of these investigations are described in the next section. It was during measurements of leaf temperature that the true situation was revealed. Having made this discovery, it was clearly necessary to repeat the whole procedure to nullify the temperature effect.

CHAPTER 12.

WIND TUNNEL YIELD EXPERIMENT 4.

12.1 Introduction

Following the discovery that ambient air was being drawn into the working section and so exposing the plants to higher temperatures than intended, it was decided to repeat the yield experiments where higher levels of turbulence had been used.

12.2 Experimental procedure

The early procedures followed the patterns of the previous experiments very closely. The nutrients supplied were exactly those in the third yield experiment when hoof and horn was excluded from the mixture and the P_1 level was 10 p.p.m.

On 21.5.1972, seeds were sown in shallow trays containing a 75% peat:25% sand mix with no added nutrients. On 4.6.1972, the seedlings were planted out into boxes and then left to grow in the greenhouse. The positions of the boxes were randomized periodically. On 1.7.1972, the boxes were transferred to the controlled temperature room again with a 12-hour day from 06.00 to 18.00 with the temperature maintained at $10^{o}C$. On 8.7.1972, the temperature was lowered to $5^{o}C$. Because of pressures on wind tunnel use, the plants were kept in the growth room until 4.8.1972, a longer period than usual. Following the normal pattern, the plants were clipped during the period in the controlled temperature room, in this case on 25.7.1972. On 4.8.1972, the nutrient levels were supplemented as necessary; only 300 p.p.m. of nitrogen were added, there being a further addition of 300 p.p.m. on 11.8.1972. Also on 4.8.1972, the initial tiller count was taken and the experiment then started. Tiller counts were again taken at weekly intervals up to the final

harvest. This started on 20.9.1972 and continued until 26.9.1972, so the average date for the harvest was 23.9.1972.

The problem of ambient air being drawn into the working section was solved by fitting a rubber seal on the rim of the box forming the floor of the working section. By manually adjusting the height of the box, an effective seal with the walls of the working section was obtained. This was carefully checked by observations of smoke flow patterns outside the tunnel.

The controls in the wind tunnel were again set to 5.5 ± 0.5°C for temperature and 80 ± 2% for relative humidity. During this experiment, the controls functioned without difficulty and any minor aberrations were easily corrected. Thus, the detailed aspects of yield can be regarded with much more certainty.

12.3 Results of the weekly tiller counts

The results of the weekly tiller counts are shown in Figures 12.1, 12.2, 12.3 and 12.4, where each value is, again, the mean of the 5 replicates and thus of 40 plants. By the start of the experiment, the average number of tillers per plant was similar to that in the previous experiment, but there was some indication that those plants with the P_2 treatment had a larger number of tillers. The pattern of growth with respect to nutrients was similar to the first and third wind tunnel yield experiments with the effect of nitrogen being especially obvious. In the N_1 treatments, the increase in tiller number was extremely slow and little affected by wind. In the N_2 treatments, where growth was much more rapid, the W_2 plants had fewer tillers by the time of the final harvest. In the P_2N_2 treatments, the initial numbers of tillers were identical so that the differences finally obtained resulted from differences in the rate of tiller production during the experimental period.

FIGURE 12.1 WIND TUNNEL YIELD EXPERIMENT 4

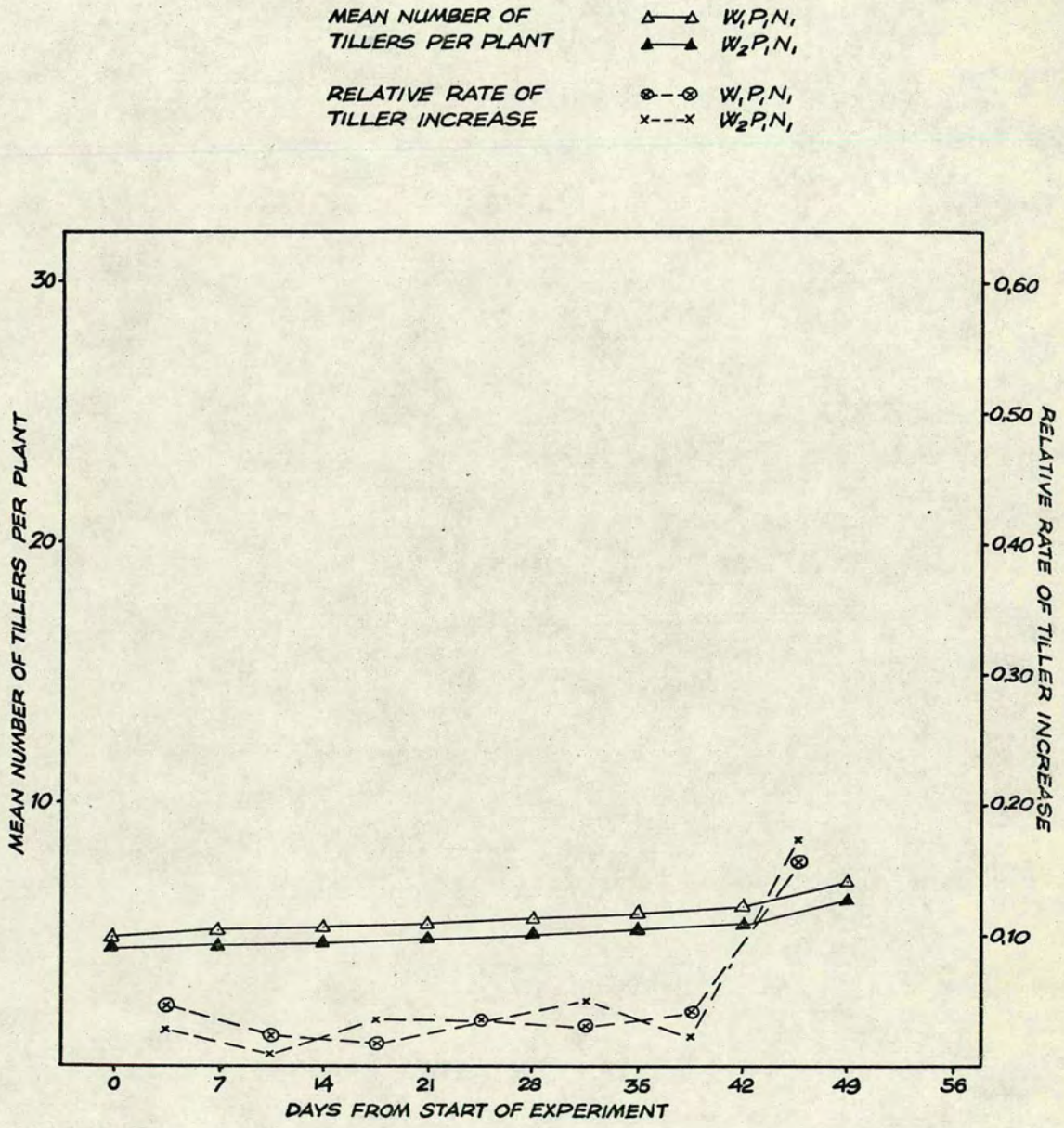


FIGURE 12,2

WIND TUNNEL YIELD EXPERIMENT 4

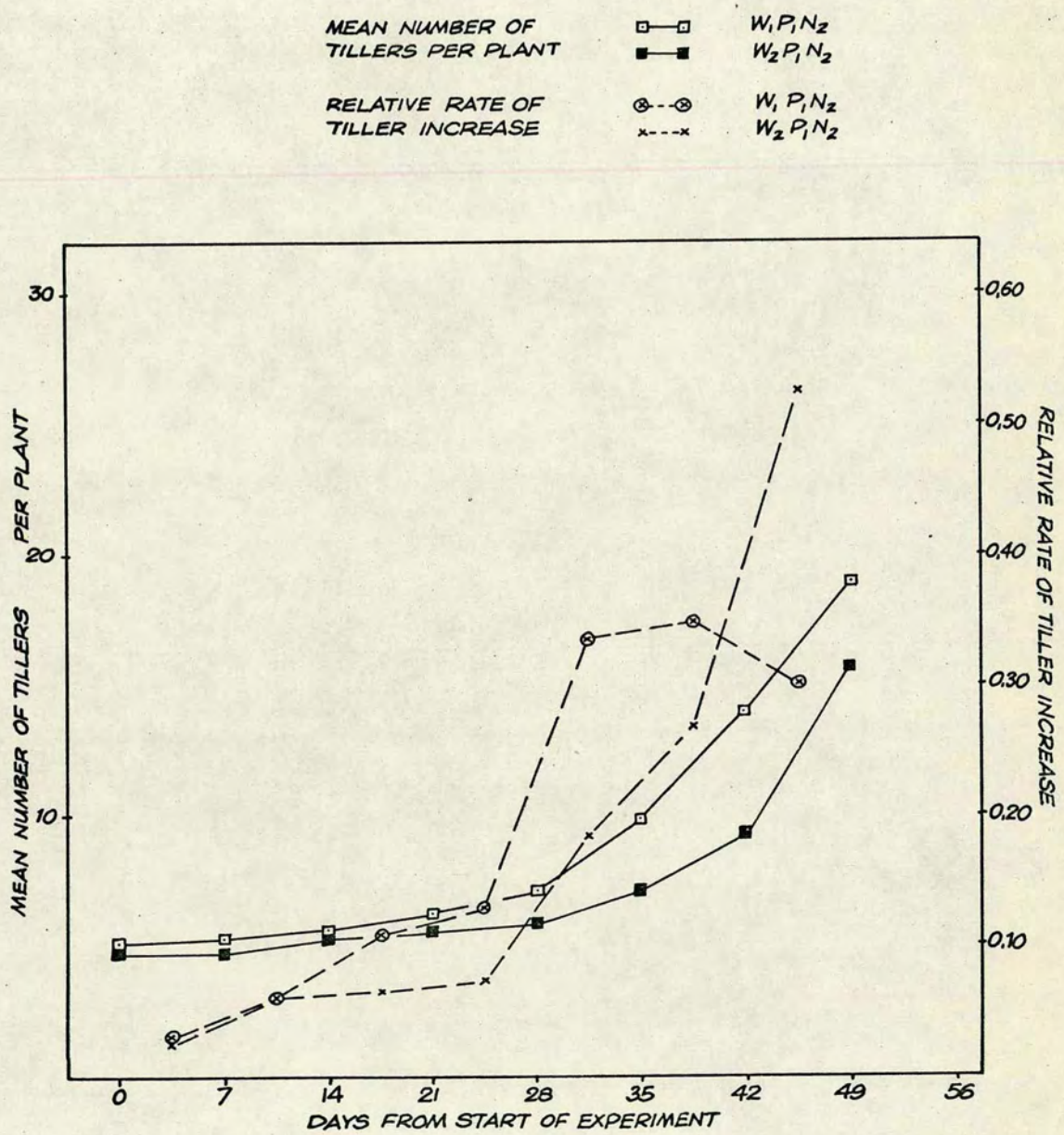


FIGURE 12.3
WIND TUNNEL YIELD EXPERIMENT 4

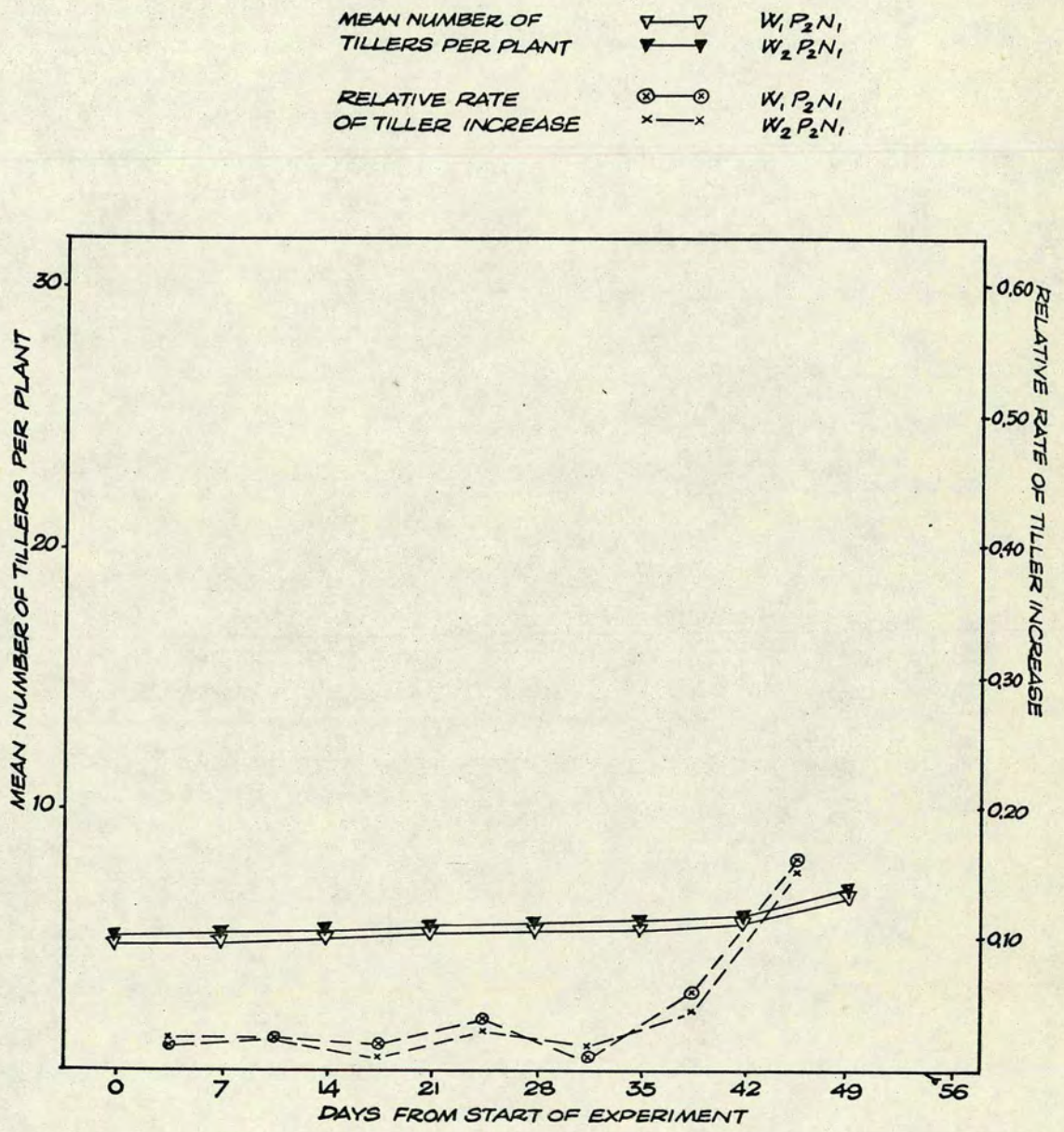
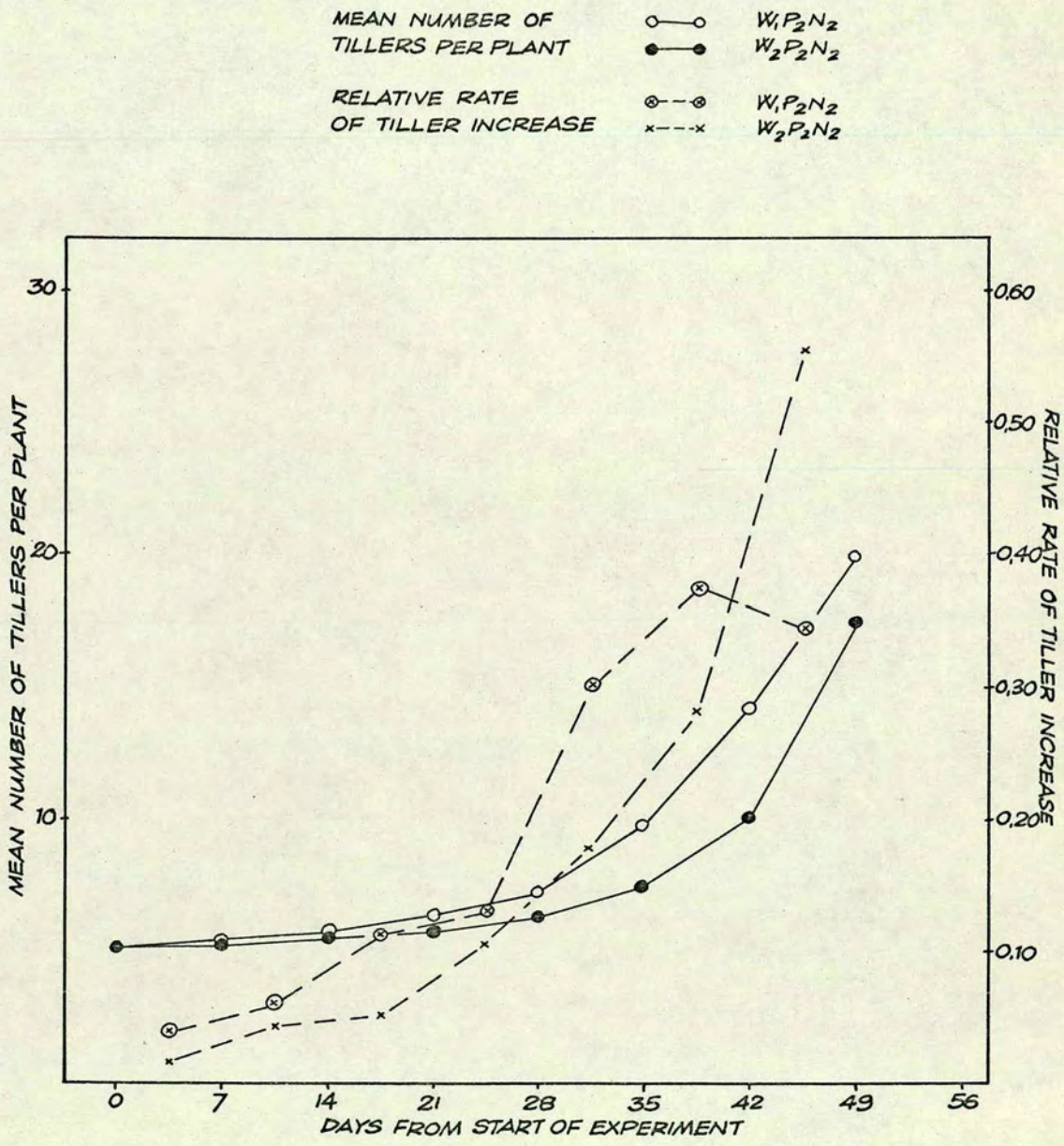


FIGURE 12,4
WIND TUNNEL YIELD EXPERIMENT 4



The analysis of variance for the final harvest shows that wind significantly depressed the rate of tiller production in both the P_1N_2 and P_2N_2 treatments.

The relative rates of increase of tiller number in the P_1N_1 and P_2N_1 treatments showed no clear effect of wind as might have been expected from the number of tillers themselves. In the P_1N_2 and P_2N_2 treatments, the growth rates rose to higher values than obtained from any of the previous experiments in both W_1 and W_2 treatments. The W_1 treatments had higher growth rates initially, but in the period between 35 and 42 days from the start of the experiment this rate tended to slow down and, in the final interval, actually fell. During this interval, the W_2 plants showed a marked acceleration in growth, which again supports the pattern of divergent and convergent phases of growth which emerged during the first wind tunnel yield experiment. It seems that at some later date, the number of tillers per plant would probably have reached a plateau value similar in both W_1 and W_2 treatments.

12.4 Results of the final harvest

The results of this, the most comprehensive of the yield experiments, are given in Tables 12.1, 12.2, and 12.3. Histograms of some of the more interesting parameters are shown in Figure 12.5.

Following the correction of the temperature anomalies, the total dry weight per plant showed an overall reduction of 7.12% due to wind, but this was only significant at the 10% level. This effect only applied in the P_1N_2 treatment and almost in the P_2N_2 treatment, where the reductions were 15.60% and 11.34% respectively. The W x N interaction was significant at 2.5% and this was probably due to the positive, but not significant effect of wind in the P_2N_1 treatment, where there was an increase of 6.12%. Nitrogen and phosphorus were both significant

WIND TUNNEL YIELD EXPERIMENT 4.

Table 12.1 Overall experimental effects : Final harvest.

Component of yield	Variable	Level 1	Level 2	% Change
TOTAL DRY WEIGHT PER PLANT (mg)	W	772	717	- 7.12
	P	712	777	+ 9.13
	N	607	883	+ 45.47
DRY WEIGHT OF SHOOTS PER PLANT (mg)	W	541	486	- 10.17
	P	488	538	+ 10.25
	N	346	681	+ 96.82
DRY WEIGHT OF ROOTS PER PLANT (mg)	W	232	232	0.00
	P	224	240	+ 7.14
	N	261	202	- 22.61
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	W	31.6	34.0	+ 7.59
	P	32.7	32.9	+ 0.61
	N	36.0	29.5	- 18.06
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	W	7.12	7.71	+ 8.34
	P	7.77	7.06	- 9.11
	N	10.42	4.41	- 57.64
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	W	256	220	- 14.06
	P	226	250	+ 10.62
	N	136	340	+150.00
DRY WEIGHT OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	W	45.52	43.95	- 3.45
	P	44.92	44.56	- 0.81
	N	39.62	49.86	+ 25.85

Table 12.1 Overall experimental effects : Final harvest (continued).

Component of yield	Variable	Level 1	Level 2	% Change
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	W	253	232	- 8.30
	P	230	255	+ 10.87
	N	173	311	+ 79.77
DRY WEIGHTS OF LEAF SHEATHS AND STEMS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	W	47.36	48.34	+ 2.07
	P	47.31	48.38	+ 2.27
	N	49.96	45.73	- 8.48
ROOT : SHOOT RATIO	W	0.56	0.60	+ 7.00
	P	0.58	0.58	+ 0.17
	N	0.84	0.31	- 62.74
LEAF AREA PER PLANT (mm^2)	W	4848	4242	- 12.51
	P	4214	4876	+ 15.71
	N	2216	6875	+210.31
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	W	0.72	0.90	+ 25.17
	P	0.80	0.82	+ 2.38
	N	0.66	0.96	+ 44.19
NUMBER OF LIVE LEAVES PER PLANT	W	25.68	20.97	- 18.35
	P	22.50	24.15	+ 7.33
	N	12.22	34.43	+181.78
INDIVIDUAL LEAF DRY WEIGHT (mg)	W	10.3	10.9	+ 5.83
	P	10.5	10.7	+ 1.90
	N	11.2	10.0	- 10.71
INDIVIDUAL LEAF AREA (mm^2)	W	184	199	+ 8.27
	P	188	195	+ 4.21
	N	182	201	+ 10.27

Table 12.1 Overall experimental effects : Final harvest (continued).

Component of yield	Variable	Level 1	Level 2	% Change
SPECIFIC LEAF AREA ($mm^2\ g^{-1}$)	W	179.78	185.23	+ 3.03
	P	180.56	184.46	+ 2.16
	N	162.89	202.12	+ 24.08
LEAF AREA PER FOLD LINE (mm^2)	W	98.28	64.98	- 33.88
	P	87.76	75.51	- 13.95
	N	43.47	119.80	+175.58
LEAF AREA PER GRAM DRY WEIGHT OF ROOT (mm^2)	W	228.18	205.46	- 9.96
	P	201.46	232.18	+ 15.25
	N	86.80	346.84	+299.58
NUMBER OF DEAD LEAVES PER PLANT	W	5.01	5.18	+ 3.50
	P	5.12	5.07	- 0.98
	N	5.50	4.69	- 14.76
NUMBER OF TILLERS PER PLANT	W	13.18	11.65	- 11.62
	P	12.06	12.77	+ 5.85
	N	6.79	18.04	+165.48
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER (mg)	W	67.9	70.8	+ 4.27
	P	67.2	71.5	+ 6.40
	N	89.6	49.1	- 45.20
DRY WEIGHT PER TILLER (mg)	W	44.1	44.9	+ 1.81
	P	43.3	45.7	+ 5.54
	N	51.2	37.8	- 26.17
DRY WEIGHT OF LEAVES PER TILLER (mg)	W	19.7	19.3	- 2.03
	P	19.1	19.9	+ 4.19
	N	20.2	18.8	- 6.93

Table 12.1 Overall experimental effects : Final harvest (continued).

Component of yield	Variable	Level 1	Level 2	% Change
NUMBER OF LIVE LEAVES PER TILLER	W	1.92	1.79	- 6.78
	P	1.84	1.87	+ 1.80
	N	1.80	1.90	+ 5.32
LEAF AREA PER TILLER (mm^2)	W	353	355	+ 0.62
	P	343	365	+ 6.35
	N	328	381	+ 16.04
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%) (REPS 1 and 2 ONLY)	W	0.35	0.36	+ 2.86
	P	0.30	0.41	+ 36.67
	N	0.29	0.41	+ 41.38
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%) (REPS 1 and 2 ONLY)	W	2.82	2.74	- 2.84
	P	2.71	2.86	+ 5.54
	N	1.09	4.48	+311.01

WIND TUNNEL YIELD EXPERIMENT 4.

Table 12.2 The effect of exposure to wind on yields : Final harvest.

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
TOTAL DRY WEIGHT PER PLANT (mg)	P_1N_1	575	572	- 0.52	+	117 mg
	P_1N_2	923	779	- 15.60		
	P_2N_1	621	659	+ 6.12		
	P_2N_2	970	860	- 11.34		
DRY WEIGHT OF SHOOTS PER PLANT (mg)	P_1N_1	335	329	- 1.79	+	71 mg
	P_1N_2	711	579	- 18.57		
	P_2N_1	353	366	+ 3.68		
	P_2N_2	763	670	- 12.19		
DRY WEIGHT OF ROOTS PER PLANT (mg)	P_1N_1	239	243	+ 1.67	-	-
	P_1N_2	212	200	- 5.66		
	P_2N_1	268	293	+ 9.33		
	P_2N_2	207	190	- 8.21		
DRY WEIGHT OF DEAD LEAVES PER PLANT (mg)	P_1N_1	35.8	36.8	+ 2.79	-	-
	P_1N_2	26.3	31.8	+ 20.91		
	P_2N_1	36.3	35.3	- 2.75		
	P_2N_2	27.9	32.1	+ 15.05		
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	P_1N_1	10.87	10.99	+ 1.10	-	-
	P_1N_2	3.73	5.49	+ 47.19		
	P_2N_1	10.23	9.58	- 6.35		
	P_2N_2	3.64	4.79	+ 31.60		
DRY WEIGHT OF LIVE LEAVES PER PLANT (mg)	P_1N_1	138	130	- 5.80	+	33 mg
	P_1N_2	355	281	- 20.84		
	P_2N_1	138	139	+ 0.73		
	P_2N_2	393	330	- 16.03		

Table 12.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
DRY WEIGHT OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT(%)	P_1N_1	41.30	39.70	- 3.87	+	3.20%
	P_1N_2	50.07	48.62	- 2.90		
	P_2N_1	39.31	38.17	- 2.90		
	P_2N_2	51.43	49.33	- 4.08		
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT (mg)	P_1N_1	162	162	0.00	+	43 mg
	P_1N_2	330	266	- 19.39		
	P_2N_1	179	191	+ 6.70		
	P_2N_2	342	308	- 9.94		
DRY WEIGHT OF LEAF SHEATHS AND STEMS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT (%)	P_1N_1	47.84	49.31	+ 3.07	-	-
	P_1N_2	46.20	45.89	- 0.67		
	P_2N_1	50.46	52.25	+ 3.55		
	P_2N_2	44.93	45.89	+ 2.14		
ROOT : SHOOT RATIO	P_1N_1	0.80	0.83	+ 3.75	-	-
	P_1N_2	0.31	0.37	+ 18.89		
	P_2N_1	0.84	0.89	+ 6.21		
	P_2N_2	0.28	0.30	+ 4.58		
LEAF AREA PER PLANT (mm^2)	P_1N_1	2253	2127	- 5.59	+	859 mm^2
	P_1N_2	6729	5747	- 14.59		
	P_2N_1	2182	2300	+ 5.41		
	P_2N_2	8230	6794	- 17.45		
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	P_1N_1	0.75	0.50	- 33.33	-	-
	P_1N_2	0.68	1.28	+ 88.24		
	P_2N_1	0.90	0.50	- 44.44		
	P_2N_2	0.55	1.33	+141.82		

Table 12.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
NUMBER OF LIVE LEAVES PER PLANT	P_1N_1	12.90	11.03	- 14.50	+	4.15
	P_1N_2	38.03	28.05	- 26.24		
	P_2N_1	12.48	12.48	0.00		
	P_2N_2	39.33	32.33	- 17.80		
INDIVIDUAL LEAF DRY WEIGHT (mg)	P_1N_1	10.6	11.8	+ 11.32	+	1.2 mg
	P_1N_2	9.4	10.0	+ 6.38		
	P_2N_1	11.2	11.2	0.00		
	P_2N_2	10.0	10.4	+ 4.00		
INDIVIDUAL LEAF AREA (mm^2)	P_1N_1	174	194	+ 11.49	+	22 mm^2
	P_1N_2	177	205	+ 15.82		
	P_2N_1	175	185	+ 5.71		
	P_2N_2	209	212	+ 1.44		
SPECIFIC LEAF AREA (mm^2)	P_1N_1	16423	16435	+ 0.07	-	-
	P_1N_2	18932	20432	+ 7.92		
	P_2N_1	15683	16616	+ 5.95		
	P_2N_2	20874	20610	- 1.26		
LEAF AREA PER FOLD LINE (mm^2)	P_1N_1	3382	5807	+ 71.70	-	-
	P_1N_2	17174	8739	- 49.11		
	P_2N_1	2912	5287	+ 81.56		
	P_2N_2	15845	6160	- 61.12		
LEAF AREA PER GRAM DRY WEIGHT OF ROOT (mm^2)	P_1N_1	9636	8853	- 8.13	-	-
	P_1N_2	32851	29245	- 10.98		
	P_2N_1	8278	7954	- 3.91		
	P_2N_2	40507	36134	- 10.80		

Table 12.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
NUMBER OF DEAD LEAVES PER PLANT	P_1N_1	5.68	5.40	- 4.93	-	-
	P_1N_2	4.63	4.78	+ 3.24		
	P_2N_1	5.38	5.55	+ 3.16		
	P_2N_2	4.35	5.00	+ 14.94		
NUMBER OF TILLERS PER PLANT	P_1N_1	7.05	6.43	- 8.79	+	1.68
	P_1N_2	19.00	15.78	- 16.95		
	P_2N_1	6.73	6.98	+ 3.72		
	P_2N_2	19.95	17.43	- 12.63		
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER (mg)	P_1N_1	81.5	89.5	+ 9.82	-	-
	P_1N_2	48.5	49.4	+ 1.86		
	P_2N_1	92.9	94.6	+ 1.83		
	P_2N_2	48.8	49.7	+ 1.84		
DRY WEIGHT PER TILLER (mg)	P_1N_1	47.5	51.4	+ 8.21	-	-
	P_1N_2	37.4	36.8	- 1.60		
	P_2N_1	53.3	52.5	- 1.50		
	P_2N_2	38.3	38.7	+ 1.04		
DRY WEIGHT OF LIVE LEAVES PER TILLER (mg)	P_1N_1	19.5	20.4	+ 4.62	-	-
	P_1N_2	18.7	17.8	- 4.81		
	P_2N_1	20.9	20.1	- 3.83		
	P_2N_2	19.7	19.0	- 3.55		
NUMBER OF LIVE LEAVES PER TILLER	P_1N_1	1.83	1.73	- 5.46	+	0.17
	P_1N_2	2.01	1.78	- 11.44		
	P_2N_1	1.87	1.79	- 4.28		
	P_2N_2	1.97	1.85	- 6.09		

Table 12.2 The effect of exposure to wind on yields : Final harvest (continued).

Component of yield	Nutrient treatment	Wind level W_1	Wind level W_2	% Change	Wind significant	L.S.D.
LEAF AREA PER TILLER (mm^2)	P_1N_1	319	333	+ 4.39	-	-
	P_1N_2	355	366	+ 3.10		
	P_2N_1	327	332	+ 1.53		
	P_2N_2	411	390	- 5.11		
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%) (REPS 1 and 2 ONLY)	P_1N_1	0.28	0.26	- 7.14		
	P_1N_2	0.32	0.33	+ 3.13		
	P_2N_1	0.30	0.34	+ 13.33		
	P_2N_2	0.52	0.52	0.00		
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT (%) (REPS 1 and 2 ONLY)	P_1N_1	1.07	1.07	0.00		
	P_1N_2	4.37	4.44	+ 1.60		
	P_2N_1	1.05	1.16	+ 10.48		
	P_2N_2	4.74	4.66	- 1.69		

WIND TUNNEL YIELD EXPERIMENT 4.

Table 12.3 Summary of analyses of variance : Final harvest.

Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
TOTAL DRY WEIGHT PER PLANT	F	3.68	5.22	93.33	0.42	6.42	0.00	0.00
	S	10.0	5.0	0.1	N.S.	2.5	N.S.	N.S.
DRY WEIGHT OF SHOOTS PER PLANT	F	9.86	8.02	368.07	0.72	11.02	1.58	0.09
	S	0.5	1.0	0.1	N.S.	0.5	N.S.	N.S.
DRY WEIGHT OF ROOTS PER PLANT	F	0.00	1.25	17.15	0.07	1.04	2.71	0.24
	S	N.S.	N.S.	0.1	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT OF DEAD LEAVES PER PLANT	F	0.92	0.01	6.89	0.11	0.95	0.09	0.00
	S	N.S.	N.S.	2.5	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	F	1.57	2.24	160.77	0.54	3.29	0.43	0.01
	S	N.S.	N.S.	0.1	N.S.	10.0	N.S.	N.S.
DRY WEIGHT OF LIVE LEAVES PER PLANT	F	19.64	8.82	635.94	0.38	16.41	5.66	0.01
	S	0.1	1.0	0.1	N.S.	0.1	2.5	N.S.
DRY WEIGHT OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	F	4.04	0.22	171.31	0.00	0.07	3.19	0.13
	S	10.0	N.S.	0.1	N.S.	N.S.	10.0	N.S.
DRY WEIGHT OF LEAF SHEATH AND STEM PER PLANT	F	4.14	5.72	171.66	1.03	6.89	0.04	0.16
	S	10.0	2.5	0.1	N.S.	2.5	N.S.	N.S.
DRY WEIGHT OF LEAF SHEATHS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	F	1.39	1.67	26.08	0.25	0.63	4.24	0.08
	S	N.S.	N.S.	0.1	N.S.	N.S.	5.0	N.S.

Table 12.3 Summary of analyses of variance : Final harvest (continued).

Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
ROOT : SHOOT RATIO	F	2.31	0.00	432.65	0.05	0.01	3.40	0.44
	S	N.S.	N.S.	0.1	N.S.	N.S.	10.0	N.S.
LEAF AREA PER PLANT	F	8.31	9.92	491.14	0.06	8.20	8.47	0.69
	S	1.0	0.5	0.1	N.S.	1.0	1.0	N.S.
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	F	0.94	0.01	2.46	0.00	7.32	0.09	0.19
	S	N.S.	N.S.	N.S.	N.S.	2.5	N.S.	N.S.
NUMBER OF LIVE LEAVES PER PLANT	F	21.55	2.64	478.84	1.43	13.83	1.26	0.07
	S	0.1	N.S.	0.1	N.S.	0.1	N.S.	N.S.
INDIVIDUAL LEAF DRY WEIGHT	F	3.43	0.58	17.37	1.50	0.04	0.80	0.40
	S	10.0	N.S.	0.1	N.S.	N.S.	N.S.	N.S.
INDIVIDUAL LEAF AREA	F	8.14	2.22	12.42	2.56	0.01	4.74	0.60
	S	1.0	N.S.	0.5	N.S.	N.S.	5.0	N.S.
SPECIFIC LEAF AREA	F	1.38	0.71	71.74	0.21	0.03	2.09	2.10
	S	N.S.	N.S.	0.1	N.S.	N.S.	N.S.	N.S.
LEAF AREA PER FOLD LINE	F	1.13	0.15	5.96	0.01	3.36	0.05	0.01
	S	N.S.	N.S.	2.5	N.S.	10.0	N.S.	N.S.
LEAF AREA PER GRAM DRY WEIGHT OF ROOT	F	2.31	4.22	302.39	0.00	1.32	7.89	0.04
	S	N.S.	5.0	0.1	N.S.	N.S.	1.0	N.S.
NUMBER OF DEAD LEAVES PER PLANT	F	0.64	0.05	13.75	1.18	1.05	0.01	0.00
	S	N.S.	N.S.	0.1	N.S.	N.S.	N.S.	N.S.

Table 12.3 Summary of analyses of variance : Final harvest.

Component of yield		Source of variation W	P	N	WxP	WxN	PxN	WxPxN
NUMBER OF TILLERS PER PLANT	F	13.92	2.96	750.72	0.92	10.72	2.09	0.01
	S	0.1	10.0	0.1	N.S.	0.5	N.S.	N.S.
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER	F	1.48	3.32	295.85	0.47	0.71	2.86	0.44
	S	N.S.	10.0	0.1	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT PER TILLER	F	0.23	2.64	78.98	0.35	0.32	0.46	0.91
	S	N.S.	N.S.	0.1	N.S.	N.S.	N.S.	N.S.
DRY WEIGHT OF LIVE LEAVES PER TILLER	F	0.39	1.67	5.29	0.39	0.46	0.16	0.62
	S	N.S.	N.S.	5.0	N.S.	N.S.	N.S.	N.S.
NUMBER OF LIVE LEAVES PER TILLER	F	9.68	0.61	5.24	0.59	0.90	0.21	0.27
	S	0.5	N.S.	5.0	N.S.	N.S.	N.S.	N.S.
LEAF AREA PER TILLER	F	0.03	3.51	20.29	0.78	0.39	2.40	0.24
	S	N.S.	10.0	0.1	N.S.	N.S.	N.S.	N.S.

F : F ratio.
S : Level of significance (%).
N.S: No significance (For levels greater than 10%).

FIGURE 12.5 WIND TUNNEL YIELD EXPERIMENT 4

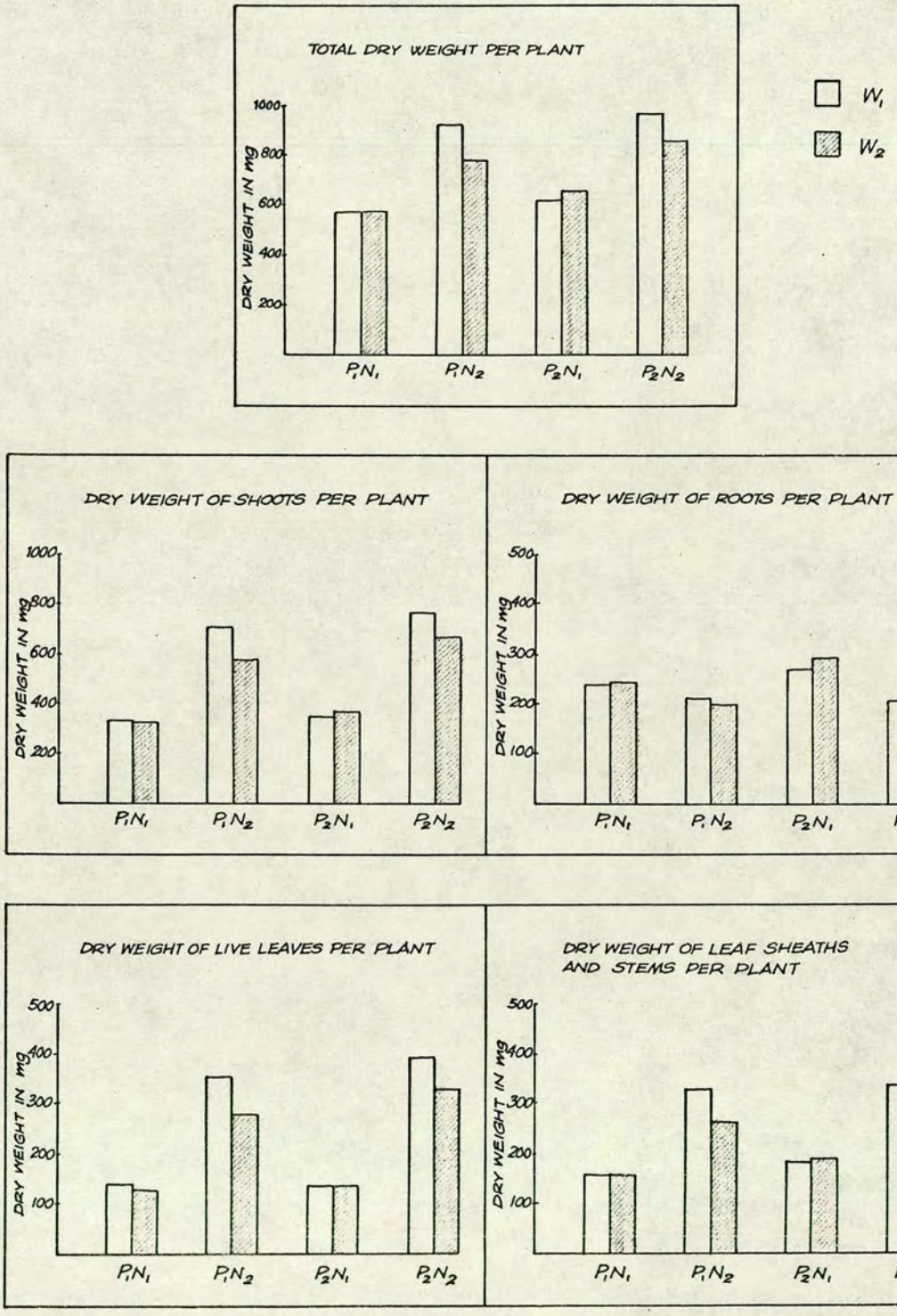
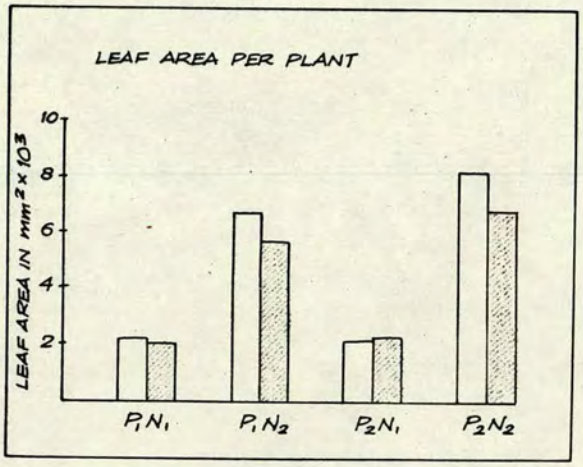
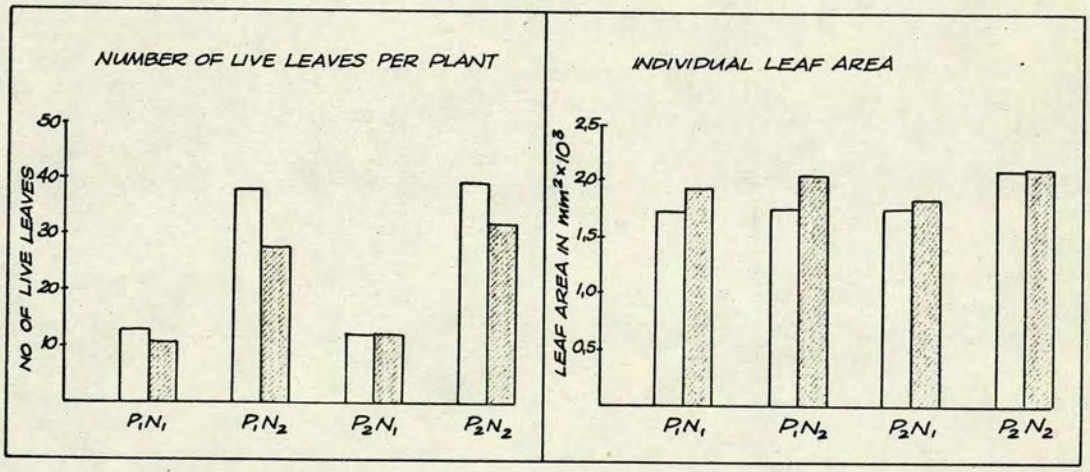
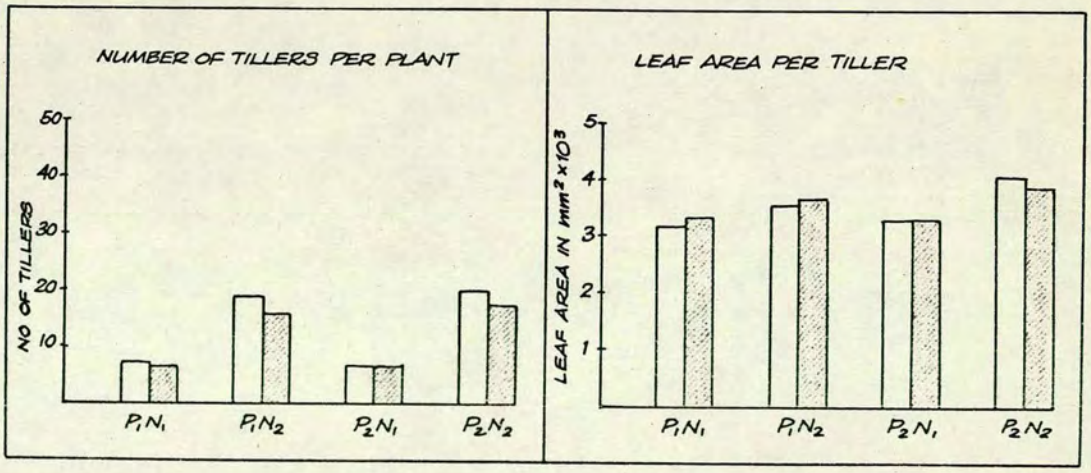


FIGURE 12.5 (CONTINUED) WIND TUNNEL YIELD EXPERIMENT 4







overall and produced increases of 9.13% and 45.47% respectively.

The dry weight of shoots per plant showed a clearer picture with the effect of wind being significant at 0.5%. This caused a reduction of 10.17% overall and, in the significant P_1N_2 and P_2N_2 treatments, corresponding reductions of 18.57% and 12.19%. The P_2N_1 treatment again showed an increase due to wind which, although not significant in itself, probably contributed to the significance at 0.5% of the W x N interaction. Both phosphorus and especially nitrogen had significant effects causing overall increases of 10.25% and 96.82% respectively.

Part of the reason for the 10% level of significance in the total dry weight data was the masking effect of the dry weight of roots, which was not significantly affected overall by exposure to wind. However, in the P_1N_2 and P_2N_2 treatments, there were still reductions of 5.66% and 8.21%. Phosphorus had no significant effect, but nitrogen reduced root production overall by 22.61%, an effect significant at 0.1%.

Examining the various components of the shoots, the dry weight of dead leaves was not significantly affected by wind nor was the proportion that this formed of the total. In the P_1N_2 treatment, wind increased the amount of dead leaves by 20.91% and caused a 47.19% increase in the proportion that this formed of the whole. It should be pointed out that the absolute proportions were very small, so that this latter figure only represented an increase of from 3.73% to 5.49%.

Wind significantly reduced the dry weight of live leaves per plant by 14.06% overall and respectively by 20.84% and 16.03% in the P_1N_2 and P_2N_2 treatments. The other treatments were not significantly different. Phosphorus also had a significant effect, causing a 10.62% increase overall. This parameter, as in the previous experiments, was strongly affected by nitrogen which produced an overall increase of 150.00%. Also, the W x N interaction was significant at 0.1%; a contributory factor here

was probably the increase of 0.73% due to wind in the P_2N_1 treatment.

Expressed as proportion of total shot dry weight, the dry weight of live leaves was slightly reduced by wind and by phosphorus (3.45% and 0.81% respectively) and increased 25.85% by nitrogen. The effect of wind was significant only at 10%, but the L.S.D. value for 5% significance was not exceeded by any of the treatment comparisons. The effect of phosphorus was not significant whilst nitrogen was significant at 0.1%.

The dry weight of leaf sheaths and stems per plant showed a similar pattern to the live leaves. Wind caused an overall decrease of 8.30%, but only the P_1N_2 treatment, where the decrease was 19.39%, was significant. In the P_2N_2 treatment, there was a decrease of 9.94%. Phosphorus increased this parameter overall by 10.87% and nitrogen by 79.77%, both effects being significant. The P_2N_1 treatment again showed a positive, but not significant effect of wind and this was reflected in the W x N interaction, which was significant at 2.5%.

The proportion that the dry weight of leaf sheaths and stems formed of the shoot dry weight was very slightly increased overall by wind, but not significantly. Again, nitrogen had more effect.

The root:shoot ratio was not significantly affected by wind or by phosphorus; in the case of wind there was an overall increase of 7.00%. Nitrogen again had a marked and significant effect decreasing this ratio by 62.74%.

In this experiment, leaf area rather than leaf length was measured and the extreme sensitivity of leaf length, especially to nitrogen noted in the previous experiments, was also found to apply to leaf area. Wind, phosphorus and nitrogen all had significant effects overall, causing a decrease of 12.51% and increases of 15.71% and 210.31% respectively in leaf area. With wind, the reduction was 14.59% in the P_1N_2 treatment and

17.45% in the P_2N_2 treatment. The P_2N_1 treatment again showed an increase due to wind and this probably contributed to the significance at 1.0% of the W x N interaction.

Since leaf area was decreased by wind, the possibility of a higher frequency of transverse fold lines per plant was examined. Although wind increased this parameter by 25.17% overall, the effect was not significant.

Another possibility considered in relation to leaf area was the effect on the number of live leaves per plant. Wind reduced leaf number significantly by 18.35% overall and by 26.24% in the P_1N_2 treatment and 17.80% in the P_2N_2 treatment. The effect of phosphorus was not significant, but nitrogen increased the number of leaves by 181.78%. The possibility that individual leaf dry weights might have been reduced by wind due to the larger number of transverse fold lines was also investigated. However, it was found that the effect of wind was only significant at 10% overall, but the effect was positive. Only in the P_1N_1 treatment was wind significant, a treatment usually having shown little response to wind. Overall, nitrogen reduced this parameter by 10.71% and this effect was significant at 0.1%.

Examination of the individual leaf area showed that this was significantly increased by exposure to wind. Overall this amounted to 8.27%, but in fact only applied in the P_1N_2 treatment, where the increase was 15.82%. In the P_1N_1 treatment, the effect, an increase of 11.49% was almost significant, which would agree with the previous results for the individual leaf dry weight. Nitrogen was significant at 0.5% and increased the area overall by 10.27%. The increase in leaf weight appeared to be negatively correlated with the number of leaves suggesting that plants with fewer leaves also tended to have larger leaves. This hypothesis is supported by comparing the values for leaf number in the various nutrient treatments with the appropriate leaf dry

weights and leaf areas. It would seem therefore, that, as a response to the reduction in number of leaves due to wind, there was some compensatory mechanism by which dry weights and areas were increased.

Another aspect in which wind could have had an effect was on the specific leaf area but, although this was much affected by nitrogen, there was no significant effect of wind or phosphorus. In fact wind only caused a 3.03% increase overall. Nitrogen, the only significant variable, caused a 24.08% increase.

Consideration has so far been given to the effect of transverse fold lines, but only when assessed on a per plant basis. It would perhaps be more relevant to consider the leaf area per fold line, a factor independent of plant size. This was a rather variable parameter, but overall, wind caused a 33.88% decrease, phosphorus a 13.95% decrease and nitrogen a 175.58% increase. Only the effect of nitrogen was significant. Closer examination of this data shows that wind increased substantially the area per fold line in the P_1N_1 and P_2N_1 treatments, but not in the P_1N_2 and P_2N_2 treatments suggesting that, at higher levels of nitrogen, the leaves were more susceptible to this kind of damage. This was confirmed by the significance, although only at 10%, of the W x N interaction.

As the leaves provide the main means of water loss from the plant and roots the main means of water uptake, the effect of wind on the balance between the two, as can be seen from the values for the leaf area per gram dry weight of root, was examined. Wind reduced this factor by 9.96%, but not significantly. The effect of nitrogen, by contrast, was significant and caused a 299.58% increase.

The number of dead leaves per plant was not significantly affected by wind, but was significantly reduced by nitrogen.

In the previous experiments, it was considered that many of the wind dependent aspects of yield were determined by the ability of the

plant to produce new tillers. In this experiment, the effect of wind on tiller production was significant overall and caused an 11.62% decrease. This only applied in the P_1N_2 and P_2N_2 treatments, where the reductions were 16.95% and 12.63% respectively. The P_2N_1 treatment actually showed an increase of 3.72% due to wind and this was partially reflected in the significance at 0.5% of the W x N interaction. Nitrogen had a particularly powerful effect and significantly increased this parameter overall by 165.48%. Phosphorus caused a 5.85% increase, but was only significant at 10%.

Examination of the dry weight of all plant material per tiller; i.e. including roots, showed no significant effect of wind, there being an overall increase of only 4.27%. Phosphorus increased this parameter by 6.40% overall and this was significant at 10%. Nitrogen caused a decrease of 45.20% and this effect was significant at 0.1%. Nitrogen also caused an increase of 165.48% in the number of tillers per plant so it would appear that the extra tillers produced were also smaller.

The dry weight per tiller showed a smaller effect of wind, which again, was not significant. Without the roots, which nitrogen has already been shown to depress considerably, the effect of nitrogen, although still significant at 0.1%, was less marked and reduced the dry weight by 26.17% overall.

The dry weight of live leaves per tiller was not significantly affected by wind or phosphorus and only at the 5% level by nitrogen. Wind caused a 2.03% and nitrogen a 6.93% reduction overall.

The number of live leaves per tiller was reduced 6.78% by wind, an effect significant at 0.5%. This only applied to the P_1N_2 treatment, where the reduction was 11.44%. Phosphorus had no significant effect and nitrogen increased this parameter by 5.32% overall, but was significant only at 5%.

The leaf area per tiller was increased very slightly by wind, but this effect was not significant. Phosphorus caused an increase of 6.35% and nitrogen an increase of 16.04%, both effects being significant.

Finally, the nutrient levels for this experiment are given at the end of the results. Time did not allow for analysis of all the samples so a statistical analysis was not possible. Instead, the means of 2 replicates only are shown.

The phosphorus levels agreed closely with those in previous experiments except in the P_2N_1 treatments, where uptake appeared to be inhibited. This was perhaps due to the particularly low level of nitrogen in the N_1 treatments. These levels were slightly lower than in yield experiments 1 and 3, but in the N_2 treatments, the levels were very similar to those in previous experiments. Wind caused an overall increase in phosphorus content of 2.86%, whilst nitrogen caused an increase of 41.38%. This result illustrates the very strong effect of nitrogen on phosphorus uptake since this increase was actually greater than that due to the higher level of phosphorus, where there was only a 36.67% increase in uptake.

Wind caused a decrease of 2.84% in nitrogen uptake, whilst phosphorus enhanced it by 5.54%. By contrast, the higher level of nitrogen increased uptake into the plant by 311.01%.

12.5 Discussion and conclusion

This experiment was the most comprehensive and reliable of the 4 attempts to assess the effect of wind on the growth of F. arundinacea. The total dry weight per plant, the dry weight of shoots per plant, the number of tillers per plant and the leaf area per plant were all significantly reduced by wind in the P_2N_2 treatment. These reductions were 11.34%, 12.19%, 12.63% and 17.45 respectively. Again, there was

evidence to suggest that the rather larger reduction in leaf area might have been due to a larger number of transverse fold lines per plant.

The responses to wind were again,only apparent at high levels of nutrient availability, especially of nitrogen. In this experiment, the differences between the P_1N_2 and P_2N_2 treatments were not so marked and in some cases the response to wind was greater in the P_1N_2 treatment. The P_2N_1 treatment frequently showed small positive responses to wind which, although not usually significant in themselves, resulted in a number of parameters showing significant W x N interactions.

The results of this experiment, together with the other yield experiments, are considered further in the next chapter.

CHAPTER 13.

GENERAL DISCUSSION OF THE WIND TUNNEL YIELD EXPERIMENTS

13.1 Introduction

The four yield experiments described in this section of the thesis each provided a very large amount of information about the responses of S.170 Festuca arundinacea to wind, phosphorus and nitrogen. The purpose of this chapter is to bring together and to evaluate this data with emphasis on the effects of wind.

In 3 out of the 4 yield experiments, wind was found to have a marked effect on growth; this effect was negative in experiments 1 and 4 but positive in experiments 2 and 3. This latter result, unexpected and at first difficult to explain, prompted much of the more investigative work described in Section 5 of this thesis. This lead to the discovery that warm air was being drawn into the working section of the wind tunnel under the W_2 conditions of yield experiments 2 and 3. Thus, to discuss these results meaningfully, it must be remembered that experiments 2 and 3 confounded effects due to wind with those due to higher temperatures.

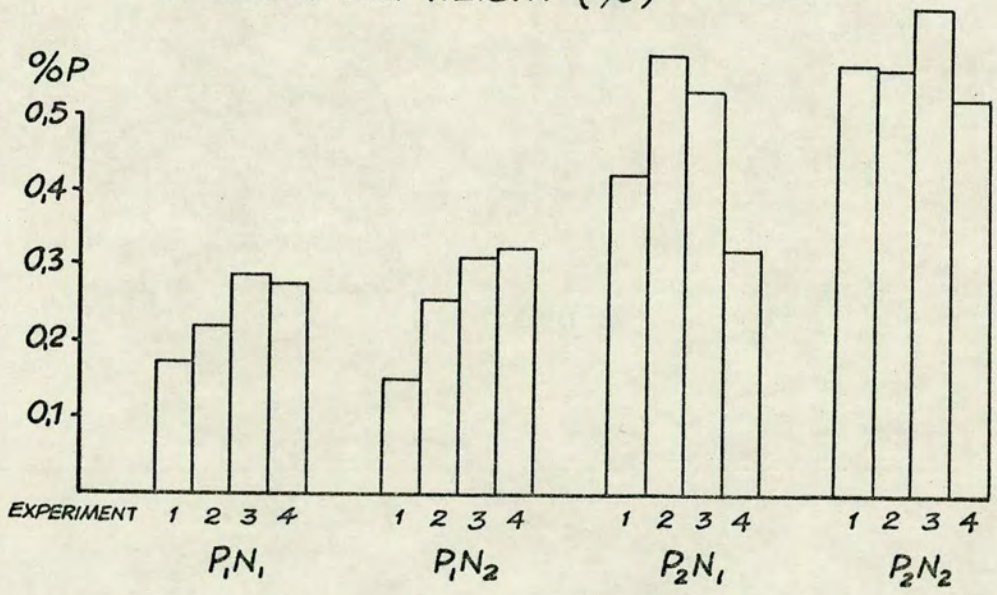
13.2 The effects of nutrients

In general, the statistically significant responses to wind occurred only where nitrogen, and to a lesser extent phosphorus, were in adequate supply. Where nutrients were limiting, there were responses to wind which were sometimes large when expressed as percentages, but which were usually too small in absolute terms for statistical significance.

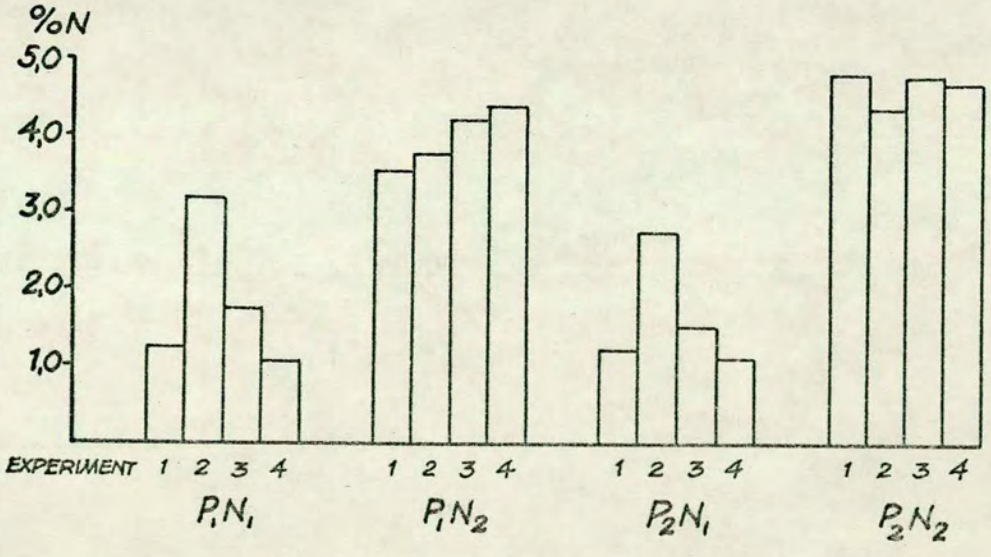
The results of the nutrient analyses are shown in Figure 13.1a for phosphorus and 13.1b for nitrogen, where each value is the mean of

FIGURE 13.1
PHOSPHORUS AND NITROGEN CONTENTS OF SHOOTS IN WIND TUNNEL YIELD EXPERIMENTS

A. PHOSPHORUS AS A PROPORTION OF SHOOT DRY WEIGHT (%)



B. NITROGEN AS A PROPORTION OF SHOOT DRY WEIGHT (%)



the W_1 and W_2 treatments. The P_1 treatments had especially low values in experiment 1 where only 5 p.p.m. were added. In the other experiments where the amount was increased to 10 p.p.m., the values were correspondingly higher. Another interesting feature was the dependence of phosphorus uptake on the level of available nitrogen. In the P_1 treatments, nitrogen had little effect, but in the P_2 treatments and especially the P_2N_1 treatments, the uptake of phosphorus was highly dependent on the availability of nitrogen. The addition of hoof and horn in experiment 2 was clearly apparent in the nitrogen levels of the N_1 plants, although not in the N_2 plants where, presumably, the uptake of nitrogen was no longer limited by availability. In the P_2N_2 treatments, the levels of nitrogen were all closely similar.

The markedly reduced effect of nitrogen in experiment 2, where the lower level was relatively high illustrates that each variable was associated with a response curve. If these experiments had been designed as 3 x 3 factorials, then it would have been possible to have gained some idea of the nature of the response curves. However, it seems from the data available that the response to nitrogen would have been much steeper than that due to wind over the ranges used in these experiments. Further, they had opposite effects with wind reducing for example the number of tillers whilst nitrogen increased it. It is clear that the responses to wind were very dependent on nutrient availability and this would seem to be an area in which further experimentation would be useful.

13.3 Overall effects of wind

The effects of the $W_1P_2N_2$ and $W_2P_2N_2$ treatments on some of the more interesting aspects of yield in each of the 4 experiments are compared in Figure 13.2. Except in experiment 2, plants with this nutrient regime showed the greatest response to wind. In experiment 2, the P_2N_1 treatment

FIGURE 13,2

COMPARISON OF WIND TUNNEL YIELD EXPERIMENTS $W_1P_2N_2$ AND $W_2P_2N_2$ TREATMENTS

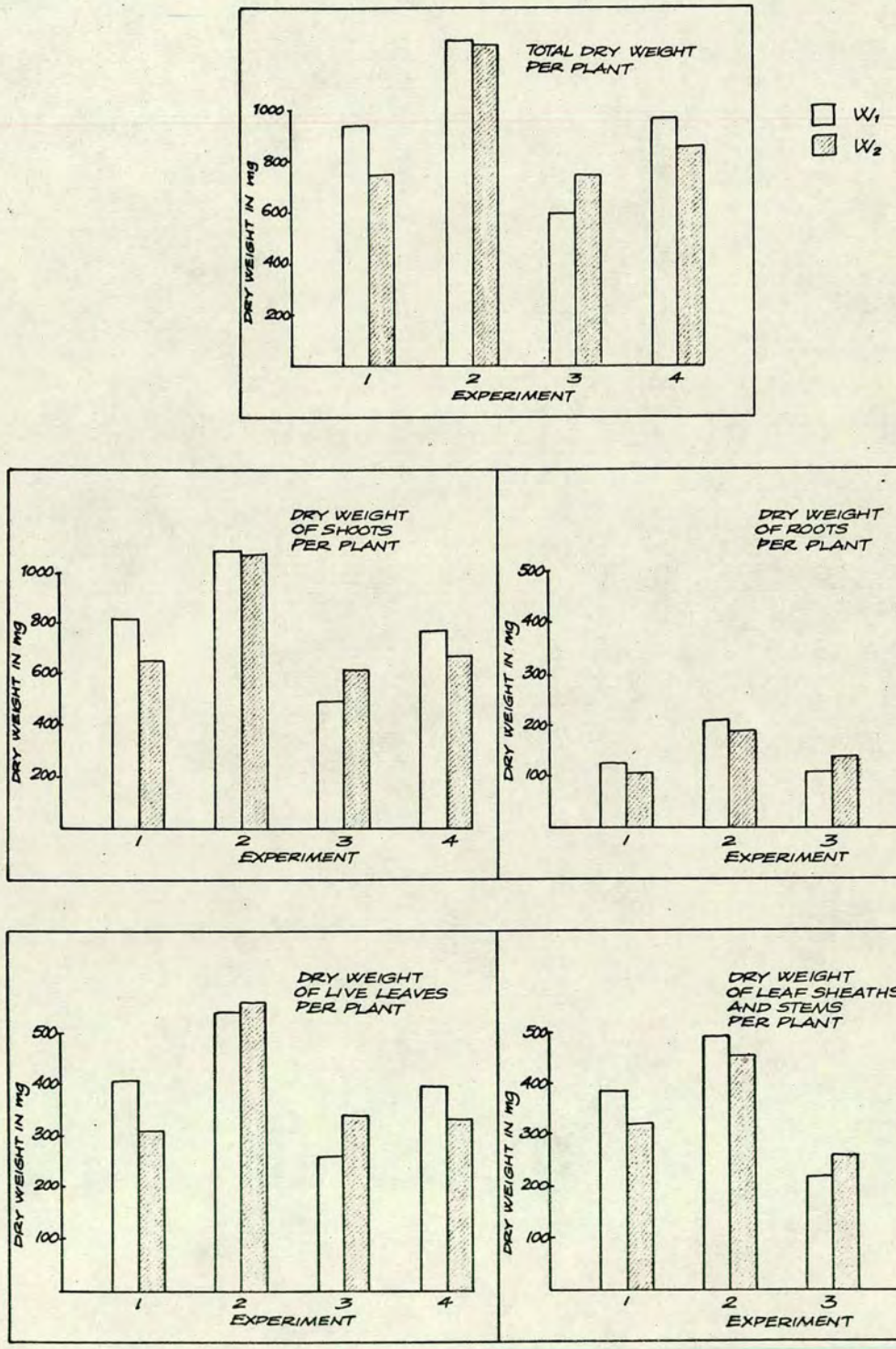
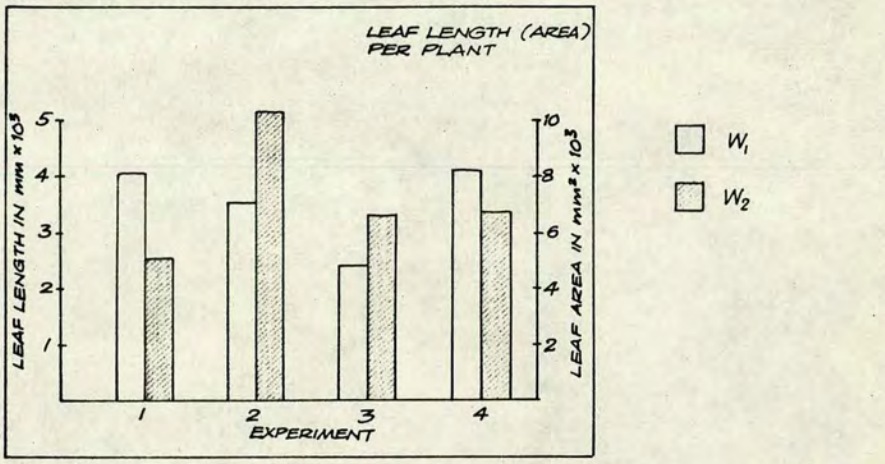
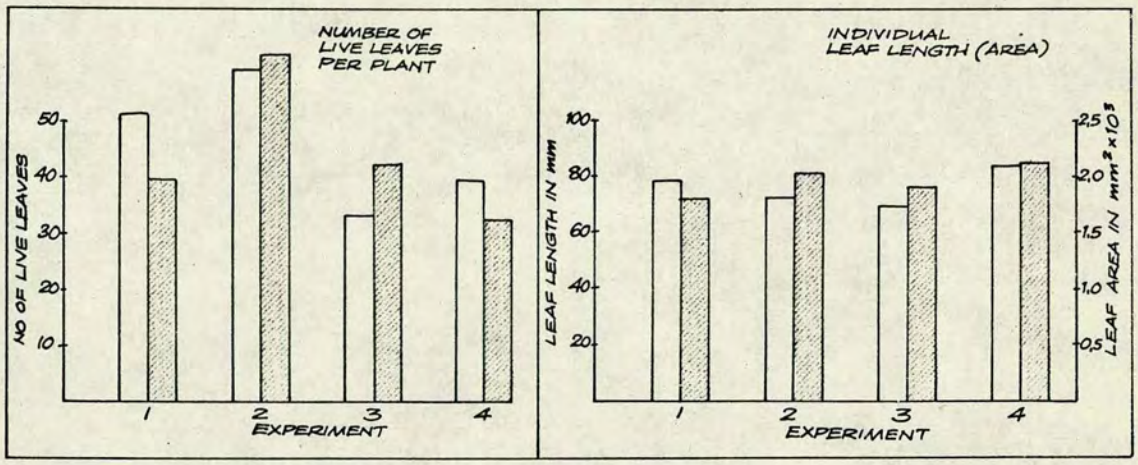
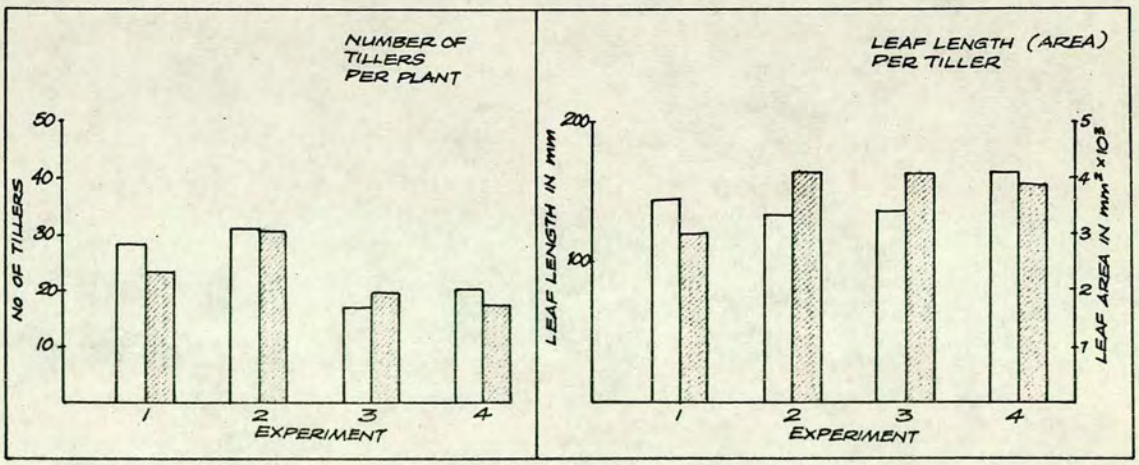


FIGURE 13.2 (CONTINUED)
COMPARISON OF WIND TUNNEL YIELD EXPERIMENTS
$W_1P_2N_2$ AND $W_2P_2N_2$ TREATMENTS







showed the greatest response, although the yields in the P_2N_2 treatment were generally higher. Initially, it was considered likely that the results for the P_2N_2 treatment could be interpreted in terms of the early convergence and later divergence situation reported by Marshall (1974) but with greater growth by the W_2 plants. However, examination of the weekly tiller counts (Figure 10.4) shows that the 2 treatments were similar throughout the experimental period although there was a tendency for any small differences to disappear by the final harvest.

The weekly tiller counts for the P_2N_2 treatments in each experiment are shown in Figure 13.3 for the W_1 treatments and Figure 13.4 for the W_2 treatments. The growth rates in the W_1 treatments should all have been closely similar but closer examination of Figure 13.3 shows that there was distinctly slower growth in the second half of experiment 3. In the W_2 treatments, the plants in experiments 2 and 3 initially had faster rates of tiller increase presumably due to higher temperatures. The growth in experiments 1 and 4 was extremely similar. The results of experiment 3,in which wind appeared to increase yields,were therefore also a reflection of the slower growth of the plants in the W_1 treatment. Perhaps a more appropriate question in this experiment is not why the W_2 plants grew faster, but why the W_1 plants grew slower.

One problem with these experiments associated with the exponential growth of young plants is to decide whether the yield difference obtained were due to wind or to initial differences in plant size. Table 13.1 shows the mean relative rates of tiller increase per week for the 4 experiments. In the P_2N_2 treatments, where this question is most pertinent, the rates were reduced by wind in experiments 1, 2 and 4 and increased in experiment 3. In experiment 2, this result was accompanied by a reversal of the initial situation by the final harvest. Thus, it appears that the final results reflected the relative rates of tiller

FIGURE 13,3
COMBINED WIND TUNNEL YIELD EXPERIMENTS

MEAN NUMBER OF TILLERS PER PLANT
TREATMENT $W_1P_2N_2$

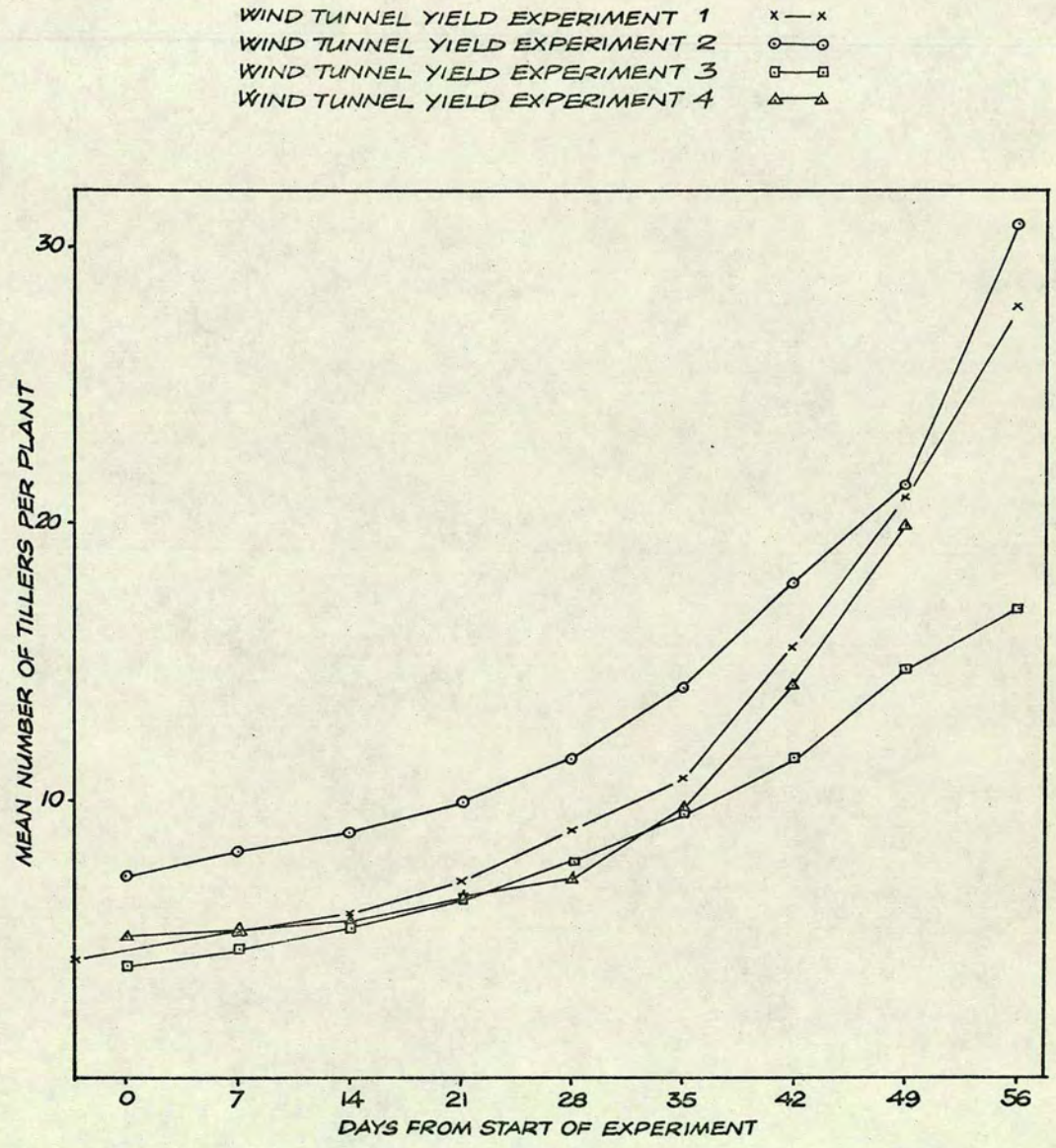


FIGURE 13.4
COMBINED WIND TUNNEL YIELD EXPERIMENTS

MEAN NUMBER OF TILLERS PER PLANT
TREATMENT $W_2P_2N_2$

WIND TUNNEL YIELD EXPERIMENT 1 ×—×
WIND TUNNEL YIELD EXPERIMENT 2 ⊙—⊙
WIND TUNNEL YIELD EXPERIMENT 3 ⊡—⊡
WIND TUNNEL YIELD EXPERIMENT 4 △—△

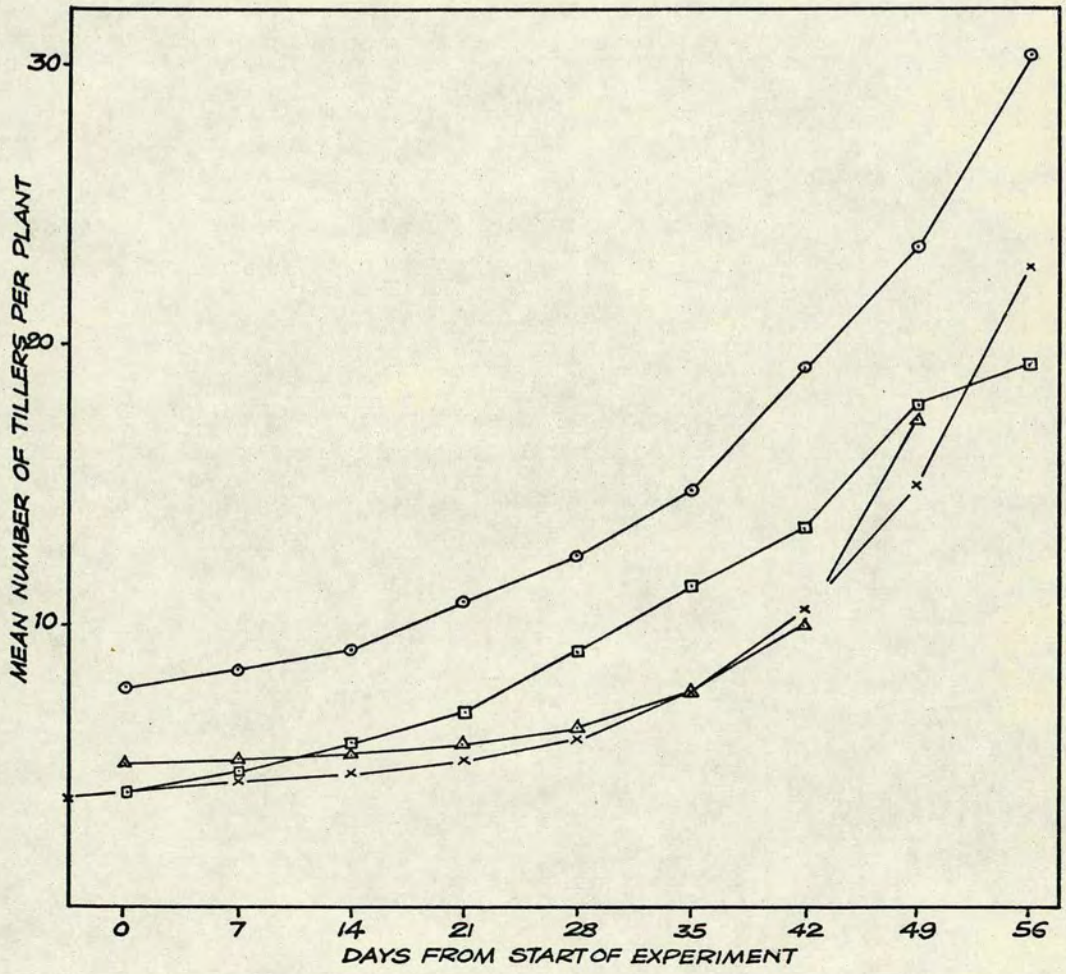


Table 13.1 Mean relative rates of tiller increase (No. of tillers tiller^{-1} wk^{-1}).

Treatment		Experiment 1	2	3	4
P_1N_1	W_1	0.129	0.172	0.125	0.051
	W_2	0.119	0.177	0.139	0.051
P_1N_2	W_1	0.157	0.176	0.161	0.187
	W_2	0.142	0.174	0.169	0.171
P_2N_1	W_1	0.103	0.149	0.094	0.047
	W_2	0.107	0.169	0.120	0.043
P_2N_2	W_1	0.233	0.179	0.178	0.194
	W_2	0.220	0.170	0.195	0.175

increase.

In experiments 1 and 4, the two main aspects of yield, the total dry weight per plant and the dry weight of shoots per plant were both reduced by wind. To consider each component of yield in turn would be unnecessarily repetitive, but it must be stressed that there was considerable variation in response to wind as is clear from closer examination of Table 13.2. For example, the large percentage reductions in total dry weight per plant or in the dry weight of shoots per plant were reflected in very similar changes in the number of tillers, but the dry weight per tiller was little affected by wind. It would seem, therefore, that the rate of production of new tillers was a key aspect in determining yield and one which was quite strongly affected by wind. There was also some evidence that wind affected the individual leaf length and the number of leaves per tiller. These 3 factors combined made the leaf length or leaf area per plant the most sensitive feature to wind.

13.4 The effects of turbulence

The effects of increased turbulence can be assessed by closer examination of experiments 1 and 4. If 4 important parameters are considered, the total dry weight per plant, the number of tillers per plant, the leaf length (area) per plant and the individual leaf length (area) (Table 13.3), it appears that there was a less detrimental effect of wind in experiment 4. In the latter experiment, the individual leaf area was actually increased in the W_2 treatment, an effect without an obvious explanation.

The difficulty of making comparisons between experiments where plants are growing exponentially has already been mentioned particularly with respect to size differences. However, reference to Figure 13.2 shows that the plant size was similar in both experiments and therefore

Table 13.2 Effects of wind on yield (% change) : Final harvests - P_2N_2 treatments only.

Component of yield	Experiment 1	2	3	4
TOTAL DRY WEIGHT PER PLANT	-19.83*	-2.26	+25.67*	-11.34
DRY WEIGHT OF SHOOTS PER PLANT	-20.20*	-0.84	+26.75*	-12.19*
DRY WEIGHT OF ROOTS PER PLANT	-17.46	-10.10	+25.45	-8.21
DRY WEIGHT OF DEAD LEAVES PER PLANT	-3.10	+17.65	-4.21	+15.05
DRY WEIGHT OF DEAD LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	+20.86	-	-	+31.60
DRY WEIGHT OF LIVE LEAVES PER PLANT	-24.16*	+3.55	+33.86*	-16.03*
DRY WEIGHT OF LIVE LEAVES AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	-4.77	-	-	-4.08
DRY WEIGHT OF LEAF SHEATHS AND STEMS PER PLANT	-17.19*	-7.76	+20.00	-9.94
DRY WEIGHT OF LEAF SHEATHS AND STEMS AS A PROPORTION OF TOTAL SHOOT DRY WEIGHT	+3.80	-	-	+2.14
ROOT : SHOOT RATIO	+6.25	-5.00	0.00	+4.58
LEAF LENGTH (AREA) PER PLANT	-37.57*	+46.15*	+38.78*	-17.45*
NUMBER OF TRANSVERSE FOLD LINES PER PLANT	+21.95	-	-	+141.82
NUMBER OF LIVE LEAVES PER PLANT	-22.78*	+4.63	+27.28*	-17.80*

Table 13.2 Effects of wind on yield (% change) : Final harvests(continued).

Component of yield	Experiment 1	2	3	4
INDIVIDUAL LEAF DRY WEIGHT	+0.0	-	-	+4.00
INDIVIDUAL LEAF LENGTH (AREA)	-7.69	+12.50*	+10.15	+1.44
SPECIFIC LEAF AREA	-	-	-	-1.26
LEAF AREA PER FOLD LINE	-	-	-	-61.12
LEAF AREA PER GRAM DRY WEIGHT OF ROOT	-	-	-	-10.80
NUMBER OF DEAD LEAVES PER PLANT	-3.51	+18.38	+1.44	+14.94
NUMBER OF TILLERS PER PLANT	-18.13*	-0.98	+14.16*	-12.63*
DRY WEIGHT OF ALL PLANT MATERIAL (INCLUDES ROOTS) PER TILLER	-1.19	-	-	+1.84
DRY WEIGHT PER TILLER	-1.37	-	-	+1.04
DRY WEIGHT OF LIVE LEAVES PER TILLER	-6.21	-	-	-3.55
NUMBER OF LIVE LEAVES PER TILLER	-6.56	-	-	-6.09
TOTAL LEAF LENGTH (AREA) PER TILLER	-16.67*	+22.39*	+19.85*	-5.11
RATIO OF NUMBER OF FLAT LEAVES TO ROUND LEAVES	+21.66	+8.50	+1.76	-

Table 13.2 Effects of wind on yield (% change) : Final harvests(continued).

Component of yield	Experiment 1	2	3	4
PHOSPHORUS CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	+1.78	+0.72	+0.94	0.00
NITROGEN CONTENT AS A PROPORTION OF SHOOT DRY WEIGHT	+6.40*	-3.82	-5.10	-1.69

* : Indicates significant effect.

Table 13.3 Overall effects of wind, phosphorus and nitrogen on 4 parameters : Final harvests.

Component of yield	Treatment	Experiment 1	2	3	4
TOTAL DRY WEIGHT PER PLANT	W	-12.40	+0.81	+10.80	-7.12
	P	+19.60	+61.46	-2.79	+9.13
	N	+45.94	+1.84	+24.60	+45.47
NUMBER OF TILLERS PER PLANT	W	-14.62	+6.35	+11.70	-11.62
	P	+48.86	+51.99	+3.52	+5.85
	N	+93.51	+4.47	+62.29	+165.48
LEAF LENGTH(AREA)PER PLANT	W	-26.02	+28.30	+23.32	-12.51
	P	+65.43	+56.89	+17.03	+15.71
	N	+145.86	+17.64	+125.75	+210.31
INDIVIDUAL LEAF LENGTH(AREA)	W	-4.17	+5.80	+4.62	+8.27
	P	+1.43	+5.80	+1.52	+4.21
	N	+11.94	+8.82	+14.52	+10.27

the diminished response of the plants in experiment 4 was likely to have been a real effect.

To assess accurately the effects of turbulence, the experimental conditions would have to be very similar. Whilst this was an important objective in the execution of this series of experiments, in practice the similarities were not as great as desirable. Examination of the nutrient levels in Figures 13.1a and 13.1b shows that in the P_2N_2 treatments, the levels of nitrogen were closely similar, but the phosphorus content was slighly less in experiment 4. Also there were other minor differences in the cultural treatments of the plants such as the duration in the greenhouse before the start of the experiment and the use of different growth rooms for the dark period, which could have had an effect on the degree of response. A better way to have investigated this would have been by using a regular alternation of turbulence levels keeping the wind speed and nutrient levels constant. It would therefore seem that the extent to which turbulence itself affected yields is uncertain, but it was unlikely to have been large.

13.5 Distinctive features of the wind tunnel yield experiments

These experiments have produced information about the responses of S.170 *F. arundinacea* which, particularly with respect to the nutrient interactions, is original. However, experiments by other workers have produced similar, if less detailed, results for other species. Where these experiments differed was in the realistic simulation of environmental conditions likely to be experienced by plants in spring in eastern Scotland and the extent to which it was possible to characterise them. The selection of suitable conditions was greatly aided by the experience gained in the field, but the creation of these conditions experimentally was achieved only through the large degree of control possible in the

wind tunnel. Where they relate to the experiments of this section, it is perhaps appropriate to summarise some of the advantages of using this wind tunnel and to outline the extent to which the environmental variables were characterised.

One great advantage of this wind tunnel is the ability to produce a low turbulence air stream with little development of the boundary layer inside the working section. This advantage seems likely to have been common to the tunnels used by Wadsworth and Tsuboi, but not to those used by Whitehead. The other experiments described in Chapter 7 were carried out with fans or with structures perhaps more accurately described as ventilated boxes rather than wind tunnels.

A second advantage lay in the use of the artificial crop kindly lent by Dr.A.S.Thom. Not only had this been the object of experimental work itself, but it was of great value in helping to create a profile in front of the experimental material. There is no mention of the use of such a device in any of the other experiments where presumably the plants projected straight into the air stream.

Apart from the provision of fetch, the creation of turbulence in a prescribed manner and its measurement at crop height is something not hitherto attempted in this type of experiment. The patterns of percentage turbulence and velocity across the floor of the working section at crop height have been described previously in Chapter 6.

In addition to the detailed observations on air flow,there were also measurements taken of air temperature, soil temperature on a diurnal basis, leaf temperature, diurnal variation of CO_2 concentration, relative humidity, radiation intensity, the spectral composition of the radiation, the levels of phosphorus and nitrogen in the soil and their subsequent levels in the plant. It was considered that by characterising the experimental conditions

as fully as possible, the significance of the results could be evaluated with much more certainty. In vindication of this approach, the anomalous temperature conditions in yield experiments 2 and 3 would otherwise have passed undetected.

13.6 Discussion and conclusions

There has been considerable research carried out on the growth of S.170 F. arundinacea (Robson, 1967, 1968, 1972, 1973 and 1974; Robson and Jewiss, 1968a and 1968b; Woledge and Jewiss, 1969). Much of this work was concerned with a comparison of S.170 with North African varieities from the viewpoint of early production. S.170 was shown to be very responsive to temperature differences especially with respect to leaf elongation. The results in yield experiments 2 and 3 would certainly confirm the sensitivity of this parameter to temperature. Similarly, the lower soil temperatures in the W_2 treatments of yield experiments 1 and 4 may also partly account for the lower yields obtained.

This aspect is not without practical significance since there is evidence of greater temperature amplitudes in sheltered areas (Caborn, 1957; Aslyng, 1958). Also, Brown and Rosenberg (1971/72) reported mean temperature increases of 1.8^{o}C in plots of irrigated sugar beets when sheltered. In contrast to yield experiments 2 and 3, higher daytime temperatures in the field would be associated with lower windspeeds.

The conclusions drawn from the field experiments were that shelter from easterly or westerly winds increased the growth of S.170 F.arundinacea. Also it appeared that this response was greater at higher levels of nitrogen and phosphorus or at higher levels of nitrogen alone. The literature review of the effects on growth of long-term exposures to wind in Chapter 7 also indicated that reductions in yield were likely to occur. Further, these reductions would be likely to be increased by increasing

velocity and turbulence and would also be markedly affected by the nutrient status of the soil.

The experimental work in this section of the thesis would support the conclusions from both the field experiments and the literature review with, perhaps, the exception of the effects of turbulence. These conclusions may be summarised as follows:

1. In conditions resembling those in eastern Scotland in spring, wind caused significant reductions in yield of up to 20% in S.170 F. arundinacea.

2. This effect of wind was most marked when supplies of nutrients, especially of nitrogen were adequate.

3. The different components of yield were affected by exposure to wind to varying degrees. One key feature was the production of tillers. The components of the tillers tended usually to be little affected by wind but any differences which did occur were magnified when viewed on a per-plant basis by changes in tiller number. Leaf length (area) per plant was found to be most sensitive to wind; in the P_2N_2 treatments, the reductions in experiment 1 and experiment 4 were 37.57% and 17.45% respectively.

4. Wind of low turbulence or of high turbulence depressed yield, but the experimental design did not allow for the differences to be adequately assessed. It appeared that the reduction in yield due to wind was diminished by increasing turbulence.

5. The controlled environment wind tunnel provided a very powerful means of assessing fully the effects of wind on the growth of S.170 Festuca arundinacea.

6. Very careful attention to experimental technique is essential to avoid spurious results when working with the controlled environment wind tunnel.

7. The substantial reductions in yield shown in these experiments are likely to be of significance for agricultural production.

8. The causal mechanisms of these reductions should be further investigated.

SECTION 5.

SUPPLEMENTARY INVESTIGATIONS INTO THE WIND TUNNEL YIELD DIFFERENCES

CHAPTER 14.

AUTHENTICATION OF THE WIND TUNNEL YIELD EXPERIMENTS

14.1 Introduction

Section 4 of this thesis described the experiments on the effects of wind, phosphorus and nitrogen on the growth and yield of Festuca arundinacea. The purpose of this section is to report on the investigations undertaken to explain why these differences in yield occurred.

Some investigations were carried out during the course of the yield experiments but, as explained earlier, because of the danger of spuriously affecting the yield results, disturbance of the experimental conditions was kept to a minimum. Further investigations were carried out on a set of experimental plants grown in the same way as before, but in which any effects on growth were of no concern. Seeds for this purpose were sown on 27.1.1972 and transplanted into boxes on 10.2.1972. After a period of growth in the greenhouse until the plants had reached the usual size of 3-4 tillers, the boxes were transferred to a controlled temperature room at $10^{o}C$ with a 12h photo-period. After one week, the plants were cut to 8 cm and the temperature then lowered to $6^{o}C$. Sufficient material was prepared to allow the working section to be completely filled when required. Since the P_2N_2 treatments in the yield experiments had shown the fastest growth rates and usually the most pronounced effects of wind, the nutrient levels were restricted to one treatment. Thus this plant material, in addition to being free from any morphological or anatomical effects due to previous wind exposure, also had greater uniformity. The air flow patterns in the working section, described in Section 3, were all obtained using this material.

14.2 Temperature measurements general

Considering the practical context of this study, i.e. with emphasis being on the resumption of grass growth in spring, it seemed logical to examine initially, the effects of temperature. Certainly at the temperature at which these experiments were carried out, approximating that critical for growth, any small differences would be expected to assume extra importance. The investigations on temperature comprised 4 aspects:

1. The use of thermohygrographs in the controlled temperature rooms to monitor the conditions prior to the start of experiments and then during the dark periods.
2. Air temperature measurements in the working section at crop height.
3. Leaf temperature measurements.
4. Soil temperature measurements at 1.3 cm depth in yield experiment 1 and 5 cm depth in yield experiments 2, 3 and 4.

The temperatures of the controlled temperature rooms used for housing the plants in the preparatory stages and later in the dark periods of the experiments were continuously monitored by 2 thermohygrographs (Casella Ltd.). As the daily and long-term variation in temperature in yield experiments 2 and 3 was found to be very small, this practice was discontinued in experiment 4. In experiments 1, 2 and 3, apart from minor effects due to changing over the boxes, the temperatures were 4.0 ± 1°C, 3.75 ± 0.75°C and 4.0 ± 1°C, respectively. The temperature during experiment 4 was also set at 4°C

and, from the soil temperature measurements, there is no reason to suspect that any aberrations occurred. Also in the other experiments, no systematic effect of time of day was detectable. This might have been expected due to the tendency of the building to heat up during the afternoons.

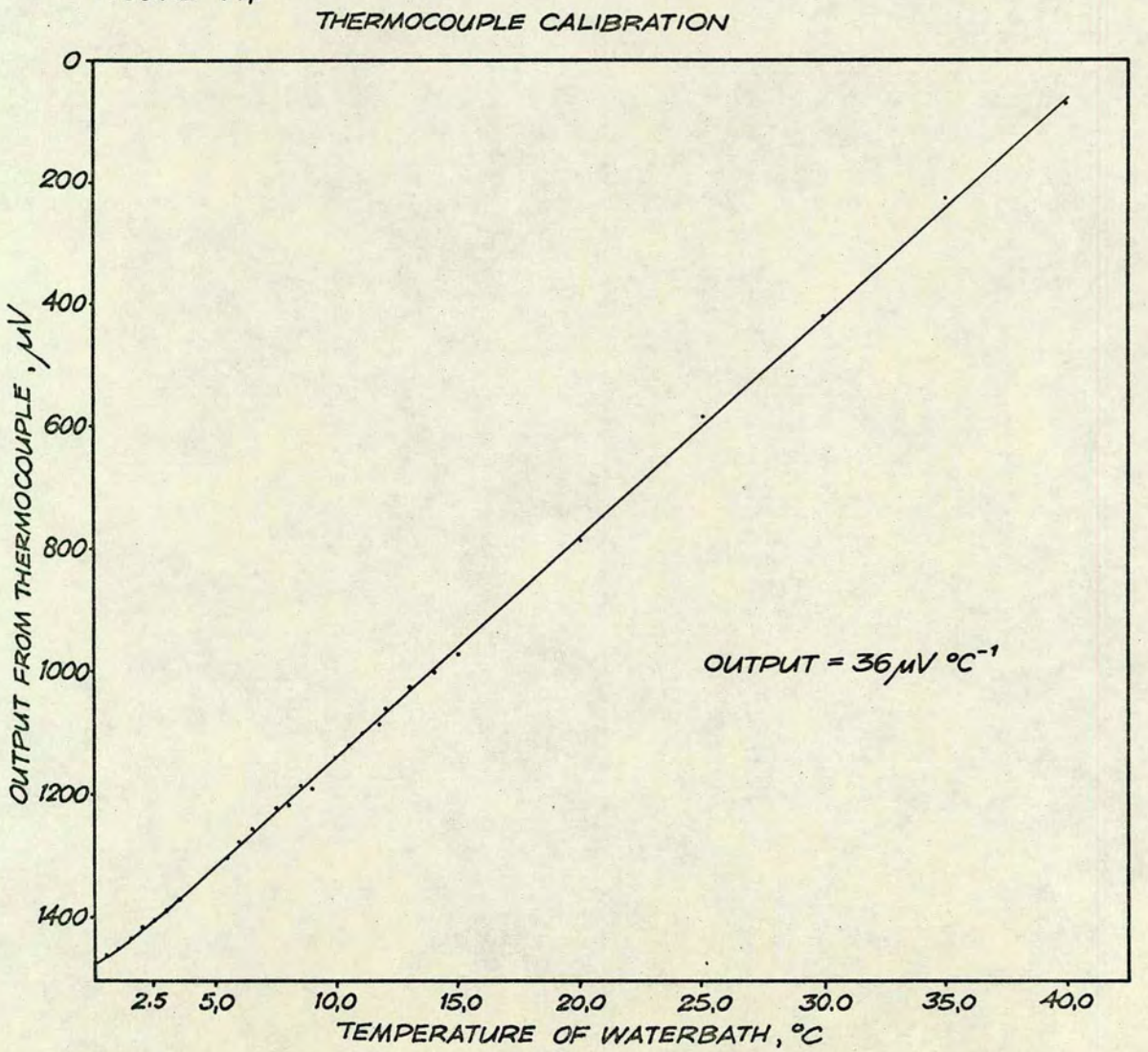
During the experiments, the setting of 5.5 ± 0.5°C in the wind tunnel was maintained throughout.

14.3 Air temperature measurements

There have been a number of studies on the effect of wind on leaf temperature and it was decided to investigate this aspect in F. arundinacea. During a preliminary investigation, before there was any attempt to seal the working section, leaf temperature was found to rise when the windspeed was increased. This implausible result suggested that the temperature conditions in the working section were other than intended and the significance of the gap between the floor of the working section and the walls was then realised. Attention was then directed to evaluating the extent of the temperature anomalies.

For this purpose the thermocouples, which had been intended for leaf temperature measurements, were used. These were welded from copper and constantan wire of 0.102 mm diameter (42 s.w.g.). The e.m.f. produced was measured on a digital voltmeter which formed part of a 100 channel data logger (Dynamco Ltd.). As no internal reference junction was available, an external unit (A.E.I. Ltd.) which maintained a constant temperature of 41.0°C was used. The thermocouples were calibrated in a water bath with a heater and stirrer in which the temperature was allowed to rise from 0°C to 40°C. The

FIGURE 14.1


THERMOCOUPLE CALIBRATION
0
200
400
600
800
1000
1200
1400
OUTPUT FROM THERMOCOUPLE, μV
OUTPUT = 36 μV °C⁻¹
2.5
5,0
10,0
15,0
20,0
25,0
30.0
35,0
40,0
TEMPERATURE OF WATERBATH, °C

calibration curve is shown in Figure 14.1. The data logger could be programmed to read over a wide range of time intervals and 0.5s was chosen. This was considered fast enough to observe any effects due to wind. The system was so arranged that a paper tape could be recorded simultaneously and this was then transcribed to give a permanent print out.

The extent of any temperature anomalies in the yield experiments was assessed by recording the changes in temperature resulting from alternating the W_1 and W_2 windspeeds. In case there were any differences due to turbulence, tests were carried out with and without the turbulence generators in position. The floor of the working section was filled, as normal, with 20 boxes of grass and a thermocouple placed sequentially in the crop at each of the 20 positions. A typical gap of about 1 cm was left between the floor of the working section and the walls. To remove any effects of radiation, the tunnel lights were switched off. The readings were taken against a background fluctuation of $\pm$ 0.5°C due to the temperature control system. The limit of sensitivity of this system was about 0.3°C.

The increases in temperature at the 20 positions under low turbulence and high turbulence conditions are shown in Figures 14.2 and 14.3 respectively. The dramatic effect on positions 17 and 20, where rises of 4.5°C and 5.5°C were recorded under the high turbulence conditions, is clearly apparent. The increases averaged over the 20 positions were 0.68°C and 1.47°C respectively. Further measurements showed similar patterns but it was found difficult to repeat these results exactly on different occasions. By closing the gap, measurements at selected positions then showed no differences in temperature.

FIGURE 14.2

THE EFFECT OF THE INTAKE OF AMBIENT AIR ON THE AIR TEMPERATURE IN THE WORKING SECTION

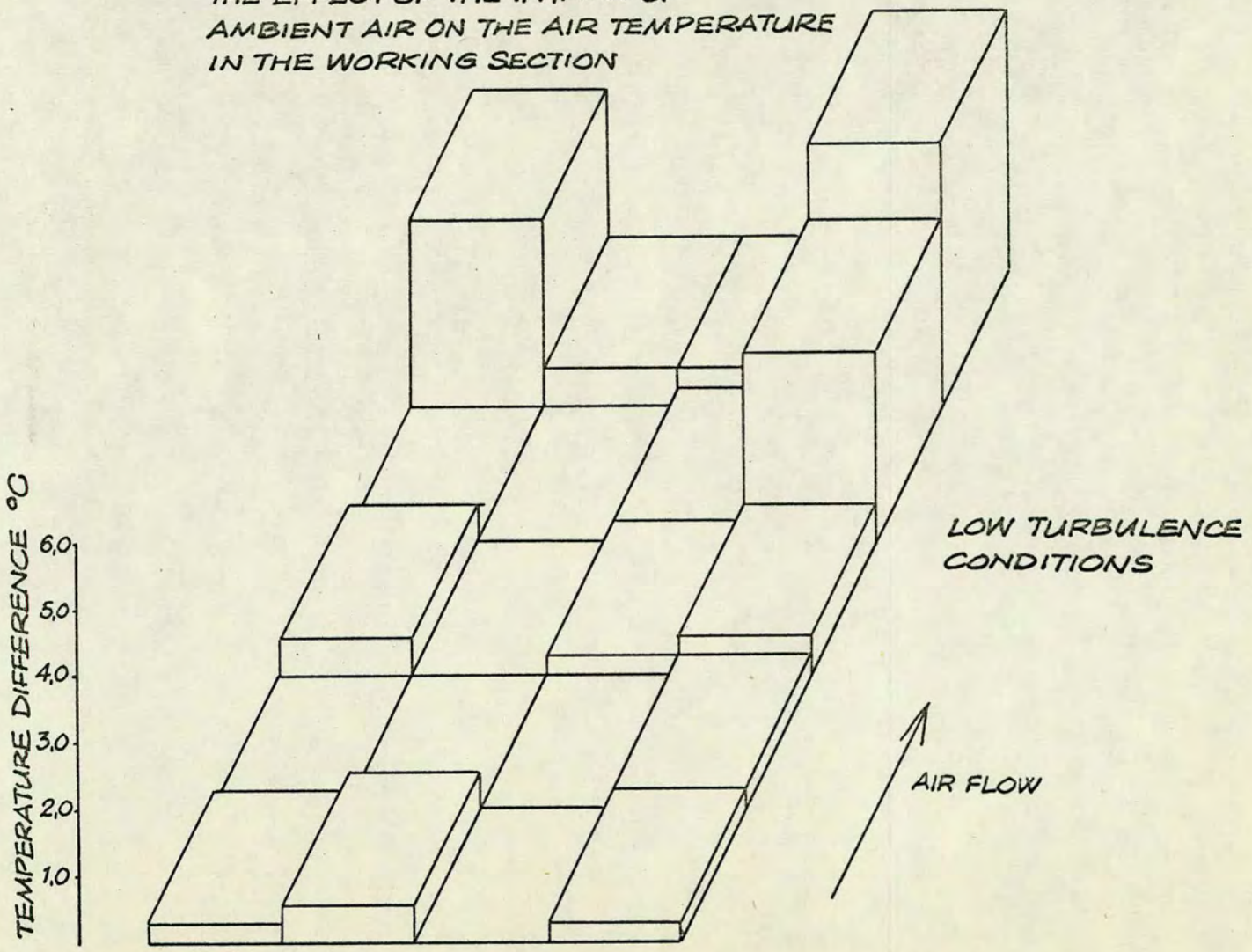
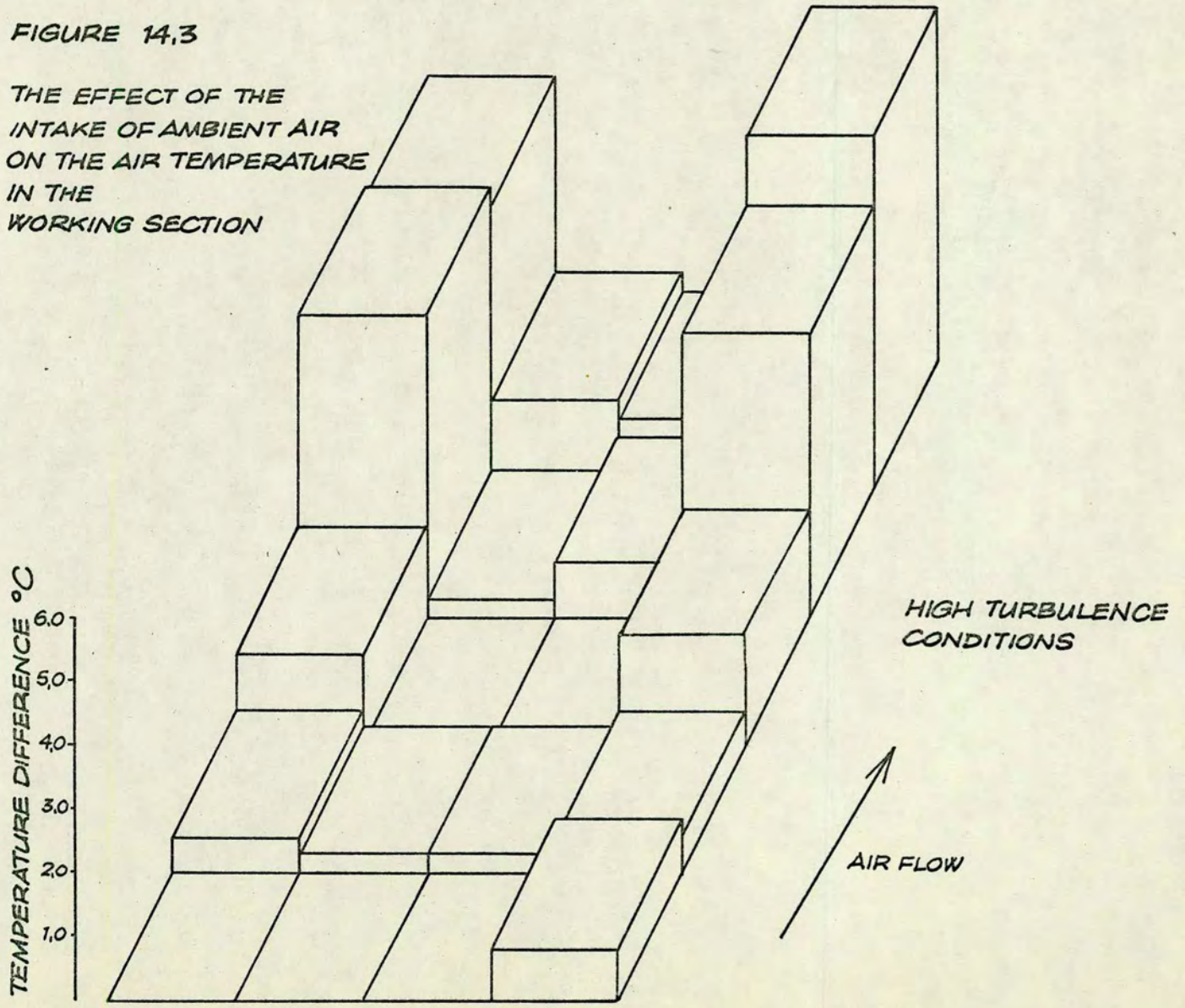


FIGURE 14.3

THE EFFECT OF THE INTAKE OF AMBIENT AIR ON THE AIR TEMPERATURE IN THE WORKING SECTION



14.4 Air flow measurements

As a final verification of this effect, the velocity of air flow across a typical gap was measured at 20 cm intervals along both sides of the working section by means of a mini-vane anemometer (Schiltknecht Ltd.). As the diameter of the anemometer head is 2 cm these results are not a true estimate of velocity. The results under low and high turbulence conditions are shown in Table 14.1.

The front of the working section had an outward air flow but a transition to an inward air flow occurred downwind. Under high turbulence conditions this transition occurred nearer to the beginning of the working section and was reflected in larger increases in temperature. The asymmetry evident in Figures 14.2 and 14.3 was also confirmed by these results. Probably the most deceptive aspect of this problem was that it was possible to feel the outflow of cold air from the front of the working section but not, of course, the inflow further along.

14.5 Leaf temperature measurements

Measurements on leaf temperature were then carried out making sure that the gap was fully closed. One of the major difficulties with leaf surface temperature measurements is to know what is being measured, an aspect highly dependent on the method of attachment of the thermocouple. It was found that if the two leads of the thermocouple were secured by sellotape towards the base of the leaf, there was suffficient elasticity in the wire to ensure that, by making a double bend, the thermocouple pressed quite firmly on to the leaf surface without any interference being produced by the proximity of any supporting mechanisms. A similar system has been used by Palmer (1966) but this was criticised by Perrier (1971) as not ensuring sufficient contact with the leaf and also because the leads to the thermocouple would experience ambient air temperatures rather

Table 14.1 Measurements of air flow through the gap in the working section in m s^{-1}.

Turbulence level	Position	Distance downwind from start of working section (cm). 20	40	60	80	100	120	140	160	180
Low	Back (Positions 4-20)	+ 0.80	+ 0.70	+ 0.40	0	- 0.40	- 0.56	- 0.63	- 0.90	- 1.20
	Front (Positions 1-17)	+ 0.82	+ 0.68	+ 0.56	0	0	- 0.46	- 0.65	- 0.82	- 0.96
High	Back (Positions 4-20)	+ 1.50	+ 0.50	- 0.90	-1.20	- 1.50	- 1.70	- 1.80	- 1.90	- 2.40
	Front (Positions 1-17)	+ 1.50	+ 0.75	- 1.00	-1.25	- 1.35	- 1.40	- 1.60	- 1.60	- 1.70

Minus sign represents inflow.
Plus sign represents outflow.

than leaf temperatures. The first objection may be less applicable when working with F.arundinacea, as it was found that, by using the adaxial surface of the leaf, which is quite strongly ridged, the thermocouples tended to lodge between the ridges. During exposure to W_2 conditions, despite considerable leaf movement, the thermocouples remained closely pressed to the leaf. A similar comparison of the effect of wind on leaf temperature was then carried out by alternating the W_1 and W_2 conditions and also using the 2 levels of turbulence. Under low turbulence conditions, of the 5 leaves observed, in 4 there was no detectable change and in 1 a fall of 0.8^{o} C. Under high turbulence conditions, of the 7 leaves observed, 5 showed no detectable change, 1 showed a rise of 0.3^{o}C and 1 showed a fall of 0.8^{o}C. It was considered that, in view of the background fluctuations in temperature, which seemed particularly marked in the case of the reduction of 0.8^{o}C in the low turbulence measurements, it would not be appropriate to place undue emphasis on the 2 appreciable temperature reductions obtained.

It was concluded from these tests that leaf temperature was little affected by wind under the experimental conditions and any effects on growth and yield would be small. The methods used were, however, somewhat crude and further investigations might usefully be undertaken, perhaps in conjunction with a hot wire probe, to determine more precisely the windspeeds over the leaf. Other studies in which larger temperature reductions due to wind have been observed have usually been with larger leaves, higher levels of radiation or lower windspeeds. It would seem likely that with a radiation level of 60.2 W m^{-2}, any heating effects would have been small and probably dissipated by convection even at the W_1 speed, so that an increase to the W_2 speed would have had no effect.

14.6 Soil temperature measurements

An initial examination of soil temperatures was started towards the end of yield experiment 1 by using 2.5 cm soil thermometers (Casella Ltd.). These were placed in the centres of the 4 boxes occupying positions 9-12 in the working section and readings taken just before the boxes were removed during a routine changeover. After this, similar readings were taken in the controlled temperature room again just prior to a changeover. The readings for each of the 4 thermometers were averaged. Table 14.2 shows the mean values obtained after 10 days in the wind tunnel and after 4 days in the controlled temperature room. The main point of interest here is the 1.23^{o}C higher temperature of the boxes removed from the wind tunnel after the W_1 treatment.

A more elaborate series of soil temperature measurements was carried out in yield experiments 2, 3 and 4 using thermistor probes (Grant Instruments(Developments)Ltd.). The probes were inserted into the boxes at 5 cm depth during the period of growth in the greenhouse. In this way, the effects of soil disturbance would have been nullified before the experiments started. Two instruments and 16 probes were available which allowed measurements to be made on 2 complete replicates. They were so arranged that 1 instrument and 1 set of probes was associated with each wind treatment. During the changing over of the boxes, the instruments were also moved and this allowed for measurements to be continuous. Both instruments were set to print out automatically every hour.

One difficulty with these instruments is the sensitivity of the measuring unit to ambient temperature conditions. Any problems that this might have caused were obviated by ensuring that both units were kept at room temperature outside both the wind tunnel and the controlled

Table 14.2 Wind tunnel yield experiment 1.
Mean Soil Temperatures at 1.3 cm depth in ^{o}C.

Location	Treatment W_1	W_2
Wind tunnel	9.39	8.16
Controlled temperature room	5.69	5.75

Table 14.3 Mean maximum soil temperatures in the wind tunnel yield experiments in ^{o}C.

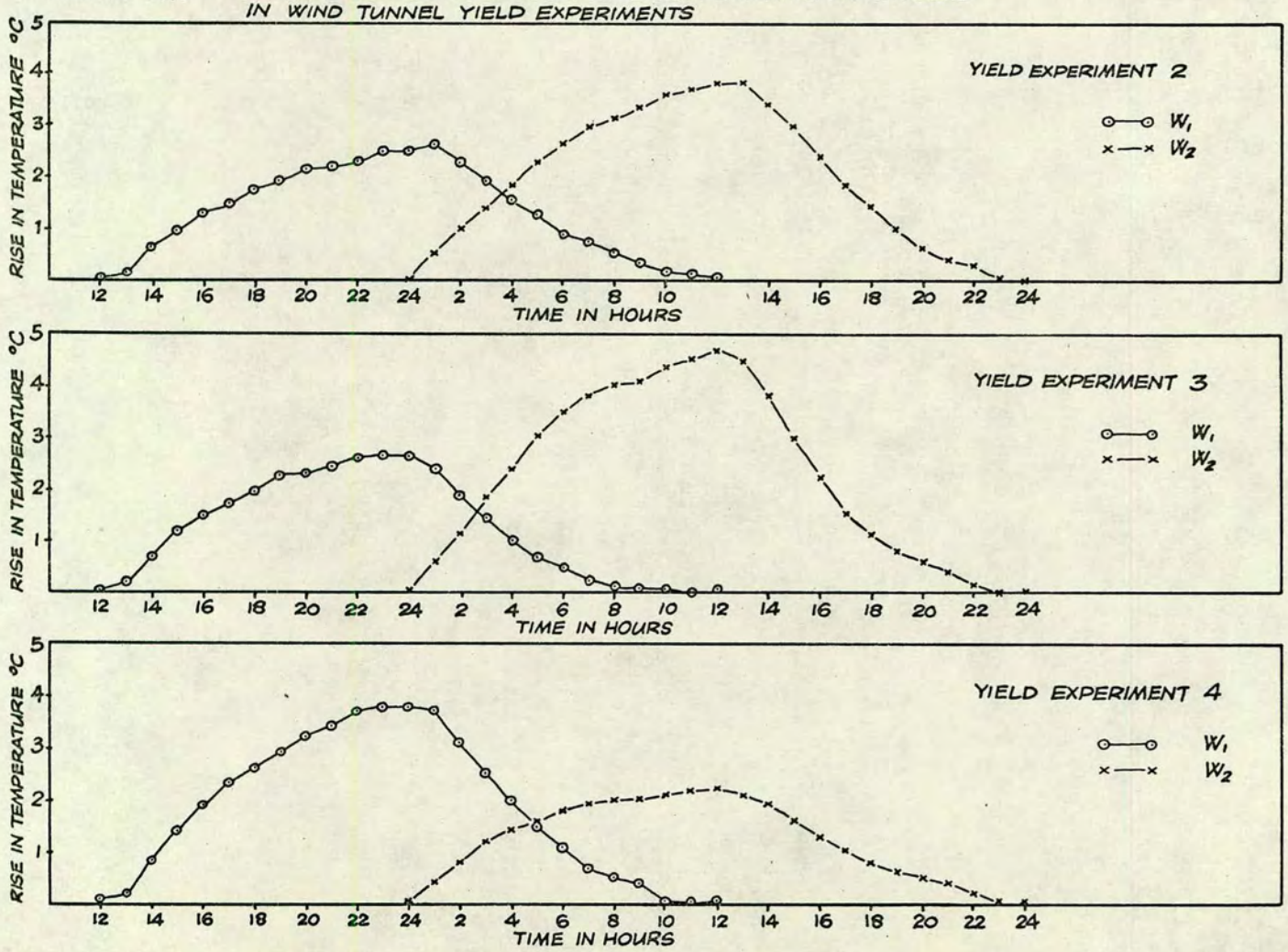
Treatment	Experiment 1	2	3	4
W_1	9.39	6.65	6.65	7.80
W_2	8.16	7.85	8.65	6.25

temperature room. Some care had to be taken in the use of these instruments over long periods as the calibration tends to be unstable. Also the electrical contacts with the "jack" plugs on the probes tended to deteriorate, a difficulty exacerbated by the regular removal and insertion necessitated by changing over the boxes. Occasionally, there were mechanical failures of the instrument itself. These difficulties resulted in a number of incomplete records but, on the whole, these instruments provided a very effective and convenient means of measuring soil temperature. Towards the beginning and end of each experiment, 2 separate sets of 5 complete days of data were extracted. After correction for any calibration differences, the data were then averaged for both periods. Rather than the absolute values, the daily amplitudes in each experiment are perhaps of more interest. These are shown in Figure 14.4 for all 3 experiments. It can be seen that the amplitude was greater in the W_2 treatments in experiments 2 and 3 and less in experiment 4. Moreover, since both treatments started at the same temperature ($4^{o}C$) after a period in the dark in the controlled temperature room, the amplitude differences were a reflection of higher temperatures in the W_2 treatment in experiments 2 and 3 and lower temperatures in experiment 4.

The final temperatures reached in each of the 4 experiments is shown in Table 14.3 for each wind treatment, although the data from experiment 1 are not strictly comparable.

These differences in temperature and in amplitude may have been due to a combination of 4 factors:

FIGURE 14.4 COMPARISON OF MEAN DAILY SOIL TEMPERATURE AMPLITUDES IN WIND TUNNEL YIELD EXPERIMENTS



1. The differences in settings between the controlled temperature room and the wind tunnel.

2. The intake of ambient air.

3. The absorption of radiation by the soil surface and differences in the rate of heat dissipation.

4. The absorption of heat through the walls of the floor of the working section.

The differences in the temperatures of the wind tunnel and the controlled temperature room probably account for the differences in maximum temperature attained in the W_1 treatments, despite the settings being the same. The differences in the W_1 and W_2 treatments are likely to have been caused by differences in the conditions in the working section, particularly in the intake of warm air. In the absence of any such intake, it would be expected that the W_1 treatments might have had higher temperatures due to radiation absorption and decreased loss of heat by convection. This occurred in both experiments 1 and 4. Consequently, increased confidence can be placed in the results of experiment 1, where there was no conscious effort made to seal the tunnel. In experiments 2 and 3, it would therefore seem reasonable to attribute the higher soil temperatures in the W_2 treatments to the intake of warm air.

14.7 CO_2 concentration measurements

Another aspect considered was the possibility that diurnal variations in CO_2 concentration could have resulted in net differences in concentration experienced by the 2 sets of plants. This aspect is perhaps one of the main dangers with this experimental system. A further closely related point is the extent to which depletion of CO_2 occurred in

the wind tunnel due to the presence of a crop and whether it applied equally to both treatments.

A model SB2 infra-red gas analyser (Grubb Parsons Ltd.) was used for this purpose and the CO_2 concentration in the wind tunnel compared against a reference concentration of 0v.p.m. The reference system was formed as a closed loop through which air was passed by a small pump (Charles Austin Ltd.). Within the loop, the air was passed sequentially through separate columns of calcium chloride, magnesium perchlorate and Indicarb soda-lime, thus ensuring removal of all H_2O vapour and CO_2. The sampling system operated in a similar manner, with the exception of the exclusion of the Indicarb and passing the sample to waste. The flow rate in both systems was adjusted to 0.6ℓ min^{-1} by means of flowmeters (G.A. Platton Ltd.).

During yield experiment 3, in the 4-day period from 10.9.1971 to 13.9.1971, prior to placing the plants in the wind tunnel, the mean concentrations within the wind tunnel fluctuated from 306 v.p.m. to 342 v.p.m. When examined as averages for the two 12-hour periods i.e. from 00.00 to 12.00 and 12.00 to 24.00, the mean values were both 322 v.p.m. On 2 complete days during the experiment, 8.12.1971 and 9.12.1971, the diurnal range was from 275 v.p.m. to 340 v.p.m. with means for the two 12-hour periods of 296 v.p.m. and 294 v.p.m. During yield experiment 4 in the 3-day period from 18.9.1972 to 20.9.1972, the diurnal fluctuation was from 294 v.p.m. to 370 v.p.m. and the means for the two 12-hour periods were 338 v.p.m. and 339 v.p.m. In the 2-day period, 23.9.1972 and 24.9.1972, when this experiment had been terminated, the diurnal range was from 326 v.p.m. to 378 v.p.m. and the means for the two 12-hour periods were 355 v.p.m. and 347 v.p.m.

These results indicate considerable differences in daily CO_2 concentrations and also that when plants were in the wind tunnel, there

was a definite depletion of CO_2. This occurred in experiment 3, despite the intake of air into the wind tunnel through the gap in the working section. A similar, but surprisingly less-marked, depletion occurred in experiment 4, where there was no intake of air. Perhaps the most important feature is the very closely similar concentrations obtained for both of the 12-hour periods rather than the absolute levels.

Further investigations of this aspect might very usefully be undertaken in the wind tunnel, but it is considered that the variations in CO_2 concentration were unlikely to have been a major factor in determining the yields in the wind tunnel experiments. The fact that experiments 2 and 3 apparently showed positive effects of wind would suggest that temperature was a far more influential factor than CO_2 concentration.

14.8 Conclusions

The following points can therefore be concluded from these investigations:

1. The results of yield experiments 2 and 3 which showed an enhanced growth due to wind were spuriously affected by the intake of warm air into the working section.
2. There is no evidence of such effects having occurred in experiments 1 and 4.
3. The effects on leaf temperature under the experimental conditions used were very small and were unlikely to have contributed significantly to the differences in yield.

4. The W_1 treatments were associated with higher soil temperatures in experiments 1 and 4 probably due to reduced convective exchange of heat. This could have accounted for some of the yield differences obtained.

5. Diurnal fluctuations in CO_2 concentration were unlikely to have affected the final yield results significantly. It appeared that the mean concentration for each of the two 12-hour periods was almost constant, although within these periods there was some variation and depletion by the growing crop. This underlines the value of having chosen 12.00 and 24.00 as times to change over the boxes.

CHAPTER 15.

THE PHYSIOLOGICAL EFFECTS OF WIND

15.1 Introduction

One of the most effective ways of verifying the effects on plant growth of an environmental factor is to examine the rate of carbon dioxide exchange. This approach has the additional advantage that the techniques involved may often indicate more fundamental causes as to why any differences in growth might occur.

There are serious technical problems associated with attempts to measure net photosynthesis *in situ* in a wind tunnel without a major disturbance of the air flow characteristics. In wind tunnel studies where no attempt is made to create a velocity profile, it can be argued that this does not matter, but the criticism that such studies,as a whole,are of diminished practical application can also be extended to similar studies on gas exchange. The review of the long-term wind tunnel studies on growth in Chapter 7 illustrated the restricted extent of experiments of this type and studies also incorporating measurements of photosynthesis are even rarer.

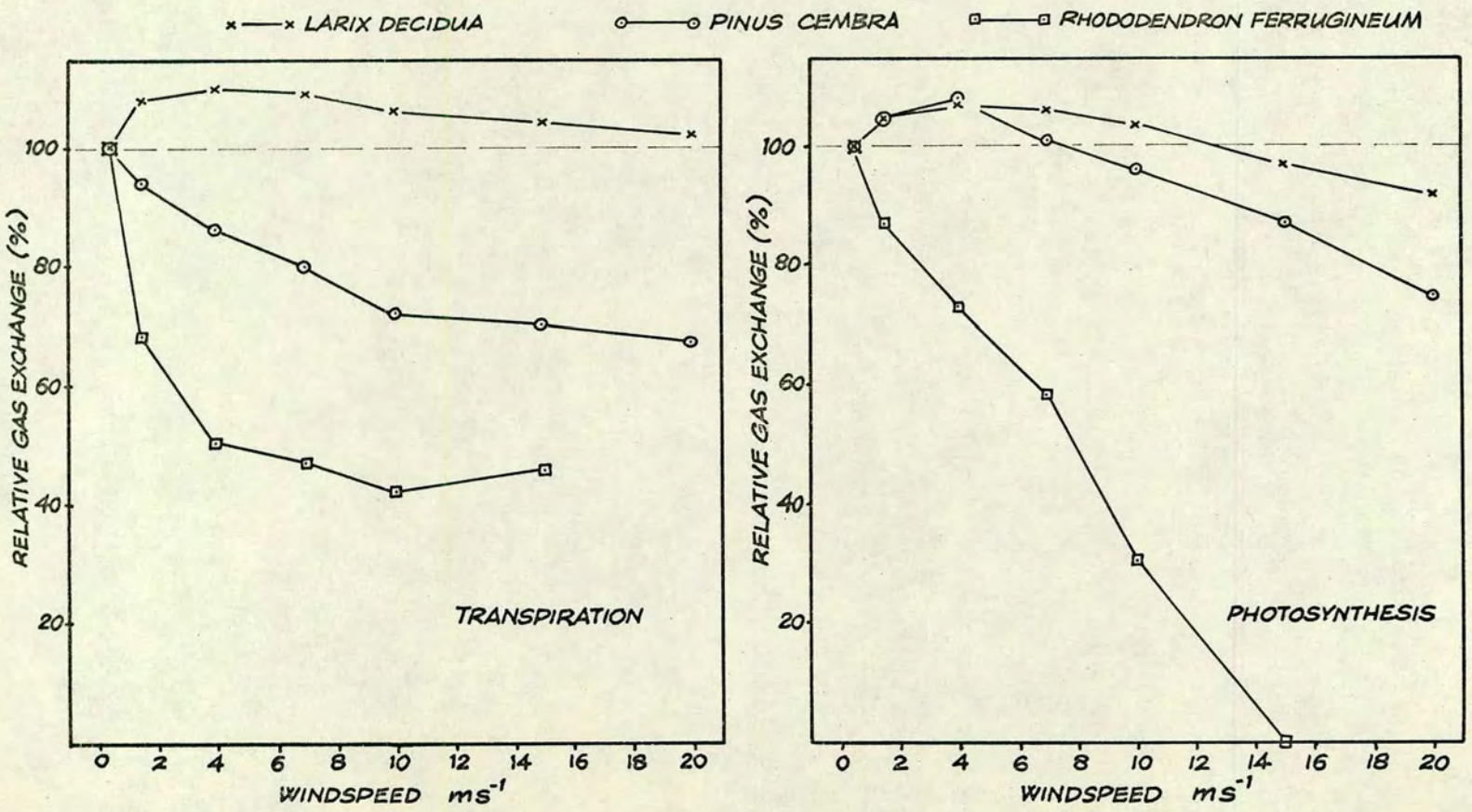
Tranquillini (1970) has reported some experimental work of this nature in the Field Station for Subalpine Forestry Research of the Austrian Federal Forestry Research Station at Innsbruck, where there are 2 wind tunnels, a large one with apparently full climatic control and a smaller version which he called a phytocyclon; this can be used as a cuvette for measurements of photosynthesis during exposure to wind. This tunnel (Tranquillini, 1966 and 1967) and its predecessor (Tranquillini, 1963), whilst having a very small working section i.e. 60 cm long x 10 cm wide x 15 cm high operates with a light intensity of up to 100,000 lux from a Xenon arc lamp. The windspeed may be varied

from 0-30m s^{-1}, the air temperature from -8°C to 40°C and the relative humidity from 15% - 95%. From photos of the apparatus, it appears that control of turbulence and development of a profile would not be possible. A unique feature is the provision of a different environment for the roots, which is achieved by allowing the pots supporting the experimental plants to project into a second chamber in which the temperature of the circulating air can be controlled from -8°C to 40°C.

In experiments using almost still air as a control, Tranquillini (1969 and 1970) examined the effect of wind on the rate of photosynthesis and transpiration of Larix decidua, Pinus cembra and Rhododendron ferrugineum. All three are species to be found in the exposed conditions near the tree line in the Tyrol. He increased wind velocity in a stepwise manner from the control of almost still air to 15m s^{-1} for R. ferrugineum and to 20m s^{-1} for L. decidua and P. cembra. His results for relative transpiration and relative net photosynthesis are reproduced as Figure 15.1. There was a considerable variation in the responses of the three species. In L. decidua velocities in excess of 12m s^{-1} were required before the positive effect of wind ceased to be apparent, whereas in R. ferrugineum, wind had a negative effect throughout and P. cembra was intermediate in response. These effects were also reflected in transpiration except in R. ferrugineum where the reduction is net photosynthesis greatly exceeded that of transpiration.

Caldwell (1970a) pointed out that it was impossible, with this experimental design, to separate the responses that Tranquillini had shown in plants exposed to the high wind velocities from any possible residual effects from exposure at lower velocities. Using the same wind tunnel, he observed the effect on relative transpiration and relative photosynthesis of R. ferrugineum and P. cembra by changing from a flow rate of 0.5m s^{-1} to 15m s^{-1}, maintaining this velocity for about 20 hours and then return-

FIGURE 15.1 TRANSPIRATION AND NET PHOTOSYNTHESIS OF YOUNG LARIX DECIDUA, PINUS CEMBRA AND RHODODENDRON FERRUGINEUM AT DIFFERENT WINDSPEEDS EXPRESSED AS A % OF GAS EXCHANGE IN ALMOST STILL AIR (100%). (AFTER TRANQUILLINI, 1970)



ing to 0.5m s^{-1}. The photosynthesis and transpiration of R. ferrugineum was reduced by about 55% and 35% respectively. In P. cembra the response was less marked and transpiration was only reduced by about 5% and photosynthesis by about 25% although in the latter case, the response was rather variable. The wind velocities used were very high but Caldwell (1970a) states that "such velocities can occur at the vegetation layer above timber line in areas where the Föhn is common".

Studies of photosynthesis and evapotranspiration were carried out by Hunt, Impens and Lemon (1967), but in a situation easier to relate to the experiments described in this thesis. They used a wind tunnel with an open circulation and having a 30 cm x 30 cm x 90 cm working section. The apparatus was housed in a greenhouse in which there was, apparently, some control over temperature. They used swards of Medicago sativa and Dactylis glomerata which were 8.1 cm and 14.0 cm high. The tunnel was set to provide velocities of 0.26 and 1.65m s^{-1} which, at crop height, amounted to 0.21 and 0.55m s^{-1}. A range of different light intensities produced corresponding variations in net photosynthesis but the mean value was greater at the higher velocity. Interestingly, there was a significant interaction between velocity and radiation intensity, reflecting the independence of these two factors at limiting light intensities. This result lends support to the Wadsworth (1959) concept of an optimum wind speed for plant growth and would also suggest that the W_1 velocity used in the experiments in this thesis was not unrealistically minimal.

15.2 The after-effect of wind on photosynthesis and transpiration

The criticism by Caldwell of the Tranquillini work raised the

possibility of an after-effect of wind. This aspect was also investigated as part of the experimental work in this thesis, but more with the object of approximating conditions in the wind tunnel. This work was undertaken with Dr. J. Grace of the Department of Forestry and Natural Resources and was subsequently published in Physiologia Plantarum. As this work was a collaborative work throughout, the paper itself is included as Appendix 1.

For convenience the abstract is included below:

> "Following a period of exposure in a controlled environment wind tunnel, the wind-treated plants showed reduced rates of photosynthesis when compared with the controls under standard conditions. Evaporation from paper model tillers was measured and the boundary layer resistance was shown to be low in all but very low wind speeds. Analysis of CO_2 and H_2O diffusion pathways indicated that mesophyll resistance in wind-treated plants was higher whilst leaf surface resistance was lower than in the controls. The high mesophyll resistance in the wind-treated plants was attributed to reduced water content."

The experimental work was carried out on plants grown as described in Chapter 13 for investigations where effects on yield were of no consequence. In the paper, the W_1 velocity is referred to as the "control" and the W_2 velocity as the "wind treatment". The control wind speed of 1m s^{-1} was not in fact different from the

overall W_1 velocity; this figure was obtained from measurements taken in the centre of the working section where this experimental material was placed.

15.3 Discussion and conclusions

The results of the paper indicated that, apart from any additional effects whilst the plants were growing in the wind tunnel, a reduction in growth due to wind would certainly be expected. The average irradiance on the floor of the working section measured at 9 positions at crop height was 48.26W m^{-2}. In Figure 1 of the paper, the differences in net photosynthesis were small and not significant at this intensity, but nevertheless were lower for the wind-treated (W_2) plants. The difference in net photosynthesis was 15.0%, which compares with a reduction of 9.8% in the relative rate of tiller increase in the corresponding P_2N_2 treatment of yield experiment 4, the only comparable rate process. This discrepancy may have been partly due to the different temperatures at which the results were obtained.

Todd, Chadwick and Tsai (1972) examined the effect of wind on plant respiration using a temperature of 28°C. Their wind chamber, a 13.5ℓ inverted bell jar, was far from being a wind tunnel, but they showed that wind could increase dark respiration in a number of species. At wind speeds of 0.9m s^{-1} and 1.8m s^{-1}, there was no measurable effect, but speeds of 3.6m s^{-1} and above caused marked increases. The respiration rate of intact wheat plants at 3.6m s^{-1}, the situation most directly comparable to the wind tunnel yield experiments, was found to be 25% higher than at 0.9m s^{-1}. Although the time scale was much shorter, they found no after-effect in respiration in the dark. If this effect were also to apply in the light, it would suggest that our studies on net photosynthesis may have under-estimated the reduction that would have

occurred whilst the plants were actually exposed to wind.

The results on after-effects have to be treated with caution when considering the wind tunnel yield experiments because of evidence of a trend towards recovery. Such a trend in magnolia respiration was also noted by Todd, Chadwick and Tsai (1972). Detached magnolia shoots exposed to a wind of 7.1m s^{-1} and prevented from fluttering returned to the original respiration rate after about 250 minutes exposure and subsequently, the rate fell further.

One of the main points of the paper was the possible relationship between rates of photosynthesis and the water content of the leaves. More recently, Jones (1973) has also reported reduced rates of photosynthesis in cotton when subject to water stress. Stomatal closure was found to be the main factor, but the activities of some photosynthetic enzymes were also reduced. These recovered less rapidly than the stomata thus producing an after-effect. Interestingly, there was some evidence of the photosynthetic system adjusting itself to water stress.

It was suggested that our reduced rates of photosynthesis might have resulted from increased water loss due to extra stomatal opening or lower cuticular resistance. One possible reason for this was the increased occurrence of mechanical damage due to the leaves rubbing over each other in the wind. The extent and nature of this mechanical damage is considered in more detail in the next chapter.

CHAPTER 16.

MECHANICAL DAMAGE IN F. ARUNDINACEA

16.1 Introduction

The work on photosynthesis and transpiration in the previous chapter made brief mention of the possible significance of mechanical damage in leaves.

Mechanical damage resulting from an exposure to wind is a commonly observed feature of higher plants and yet it has received comparatively little serious attention. Amongst the many factors which may determine the extent to which damage occurs, the morphology of the plant is very important, plants with structures offering a high wind resistance being especially susceptible. Such situations obtain in many horticultural crops where the economic yield may be critically dependent on the avoidance of mechanical damage. Wind damage in horticultural crops has recently been comprehensively reviewed by Waister (1972b) and he suggested that the comparatively slight attention given to mechanical damage may be a reflection of its obvious nature. In strawberries, Waister (1972a) reported physical damage in the form of blackening of parts of the leaf laminae and of the sides of the petioles as a result of rubbing or of repeated flexing. Before considering the adverse effects of damage, it is perhaps worth noting that Taylor and Sexton (1972) have suggested that leaf tearing in bananas, such as frequently occurs at right angles to the midrib,may have positive advantages in heat exchange and may prevent the occurrence of excessively high leaf temperatures.

Whilst information on horticultural crops may be limited, Marshall (1967) noted that it is,nevertheless,more readily available than on grasslands and field crops. Whilst the lodging of cereals is perhaps the most frequently observed form of mechanical damage in the Gramineae, other

aspects have also been reported. In rice, bruising of the leaf tips and intense desiccation of the bent stems was noted by Tsuboi (1961) and in wheat, Sill, Lowe, Bellingham and Fellows (1954) found that leaf contacts during strong winds produced abrasions. Aston and Bradshaw (1966) examined population differentiation in Agrostis stolonifera from a region of exposed cliff and pasture and their observations on stolon length and the frequency of occurrence of blue-green individuals are of particular interest. They found that stolon length was inversely related to the degree of exposure and that if plants with long stolons were subsequently exposed to strong winds, mechanical damage in the form of leaf tearing and breaking of the stolons resulted. Blue-green individuals were found to occur more frequently in more exposed areas; an exposed cliff population was composed entirely of blue-green plants, an exposed pasture had 20% green plants and sheltered pasture and stream populations were composed entirely of green plants. Similar colour variations occur between coastal and inland varieties of Festuca rubra ssp. rubra (Hubbard, 1968). It seems likely that such colourations are a reflection of differences in the nature of the cuticle. Hodgson (1973) demonstrated that there was considerable variation between ecotypes of Cirsium arvense with respect to the amount of lipid present on the leaves. This was also greatly affected by the environment of the plants but, whilst the degree of exposure was implicated as a cause, this could not be established with certainty.

The purpose of this chapter is to describe the investigations carried out on mechanical damage in Festuca arundinacea. This seemed to take the form of an increased frequency of transverse fold lines and an increased frequency of abrasion marks on the leaf surface. Plate 16.1 shows leaves of F. arundinacea taken from a $W_1P_2N_2$ treatment. For comparative purposes, Plate 16.2 shows the effects of a transverse fold line and also of the

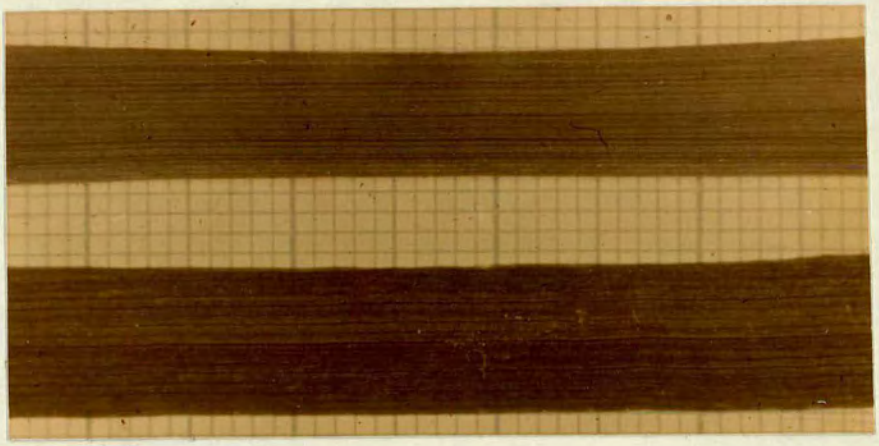


Plate 16.1 Laminae of S. 170 Festuca arundinacea grown under $W_1P_2N_2$ conditions ($0.6m\ s^{-1}$).

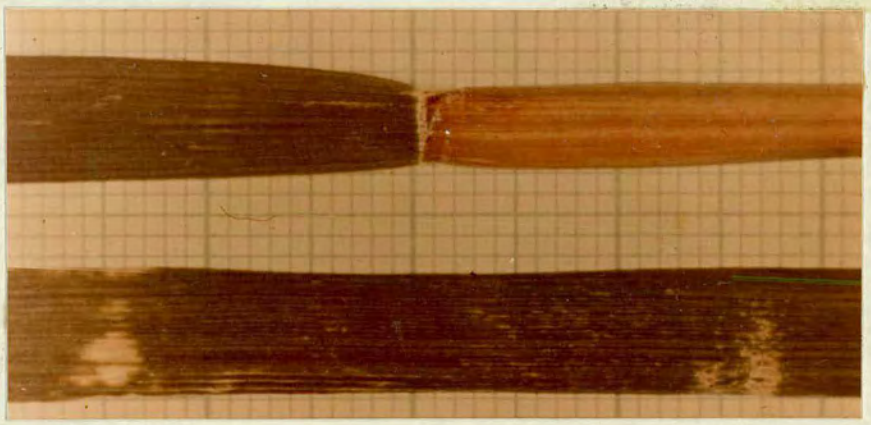


Plate 16.2 Laminae of S.170 Festuca arundinacea grown under $W_2P_2N_2$ conditions, ($3.5m\ s^{-1}$). The upper leaf shows a transverse fold line and its effect on the rest of the lamina. The lower leaf shows two areas of severe surface abrasion.

abrasion marks on leaves from a $W_2P_2N_2$ treatment.

16.2 Transverse fold lines

Once a transverse fold line is formed, the tissue beyond may show signs of wilting, chlorosis and sometime necrosis. Occasionally, defoliation beyond the fold line may occur due to particularly violent fluttering. This motion has been studied in more detail by Grace (1974) with time lapse photography and he was able to show the wide variation in position and degree of flexing that may be exhibited by a single leaf in a very short period of time. In their studies on respiration, Todd, Chadwick and Tsai (1972) also described a whipping motion of the grasses occurring as a result of their flexible stems.

In Chapter 8, details were given on how this parameter was measured and some mention has already been made of the results in the respective yield experiments. The purpose of this chapter is to consider this aspect overall.

After counting the number of fold lines per leaf, the results were then transformed to specific fold line frequencies, i.e. the number of fold lines per gram dry weight of laminae. This transformation takes account of the considerable variation in size that occurred between plants in different experiments and with different nutrient levels. The results for each of the 4 experiments are shown in Table 16.1, where it can be seen that, in all cases except in the P_1N_1 and P_2N_1 treatments of experiment 4, the W_2 treatments had higher specific fold line frequencies. An analysis of variance on the specific fold line frequency ratios associated with each nutrient level showed that there were no significant differences between nutrient levels. Considering only the P_2N_2 treatment, that in which most of the yield differences occurred, the W_2 plants had consistently higher specific fold line frequencies, an effect significant at the 2.5%

Table 16.1 The effect of wind on the specific fold line frequency and specific fold line frequency ratio of S.170 *F. arundinacea* Schreb.

Treatment and ratio	Experiment 1	2	3	4	Mean
$W_2P_1N_1$	9.93	19.63	11.87	4.03	11.37
$W_1P_1N_1$	8.38	7.98	8.38	5.47	7.55
RATIO W_2:W_1	1.18	2.46	1.42	0.74	1.50
$W_2P_1N_2$	18.69	13.42	11.22	4.71	12.01
$W_1P_1N_2$	10.25	5.99	8.60	2.04	6.72
RATIO W_2:W_1	1.82	2.24	1.30	2.31	1.92
$W_2P_2N_1$	16.68	22.82	9.21	3.54	13.06
$W_1P_2N_1$	8.06	8.58	5.18	6.50	7.08
RATIO W_2:W_1	2.07	2.66	1.78	0.54	1.80
$W_2P_2N_2$	9.39	18.30	13.58	4.17	11.36
$W_1P_2N_2$	3.63	11.37	7.37	1.51	5.97
RATIO W_2:W_1	2.59	1.61	1.84	2.76	2.20

level. The level of significance would appear to have been reduced by the rather large variation between experiments.

In experiment 4, the only one for which leaf area measurements were available, there was an average of 1 fold line per 158.5 cm^2 in the $W_1P_2N_2$ treatment and 1 fold line per 61.6 cm^2 in the $W_2P_2N_2$ treatment.

In experiments 1, 2 and 3, the number of fold lines was recorded for each leaf individually and so it is possible to evaluate the number of leaves that were actually affected. There appeared to be a tendency for leaves having fold lines to have more than 1 so that the proportion of leaves per plant was usually quite small. Table 16.2 shows the percentage of leaves in the first three experiments which had 1 or more fold lines.

If mechanical damage does adversely affect the growth of grasses, it would be useful to have a simple objective means of assessing it. In plants with larger structures and more obvious manifestations of damage, it may be feasible to develop a subjective scoring system,for example,of the type used in crop damage assessment in herbicide screening. In grasses where such damage is far less obvious, it is suggested that the specific fold frequency ratio might provide a simple means of assessing damage at least under experimental conditions. Reference to Table 16.2 shows that the percentage of leaves involved is small and this would have to be considered in any sampling procedure adopted.

16.3 Surface abrasions

The abrasion marks on the leaf surface were investigated by the use of a stereoscan electron microscope on material taken mostly from the P_2N_2 treatments during the final harvest in yield experiment 4. During the destructive harvest, samples of representative leaves were selected and placed in a model EF2 freeze-drier (Edwards High Vacuum Ltd.) for 24h at a chamber temperature of $-20^{o}C$ and a vacuum of 0.1 Torr. They were then

Table 16.2 The effect of wind on the percentage of leaves of S.170 F. arundinacea (Schreb.) with one or more fold lines.

Treatment	Experiment 1	2	3	Mean
W_2	5.03	13.46	9.45	9.31
W_1	2.69	7.99	5.08	5.25

stored in a desiccator. In preparing material for examination, small areas of leaf were mounted on a stub, carbon coated in a vacuum evaporator (A.E.I. Ltd.) and then coated with a 200 - 300 Å layer of gold palladium (Balzer Ltd.). The samples were then observed in a Mark 2A Stereoscan electron microscope (Cambridge Instruments Ltd.).

The results of the surface examination of the leaves by the stereoscan electron microscope are shown in Plates 16.3 and 16.4. To facilitate the interpretation of the surface structures, reference can be made to studies of the anatomy of F. arundinacea by Warnke (1911), Metcalfe (1960) and Badoux (1971). This species has a strongly ridged adaxial surface and a far less structured abaxial surface. In the areas examined, there seems to be more obvious damage on the adaxial surfaces. This may be due to the tendency of the edges of some mature leaves to curl abaxially, thereby protecting the abaxial surfaces against rubbing by other leaves. The W_1 abaxial surface is shown in Plate 16.3A and the W_2 surface in Plate 16.3B, the main difference being the less-pronounced ridging on the W_2 surface. Plate 16.3C shows a W_1 adaxial surface and the damage caused by abrasive contacts between leaves in Plate 16.3D. This damage is shown in greater detail in Plates 16.3E and 16.3F, the tearing of the surface cells on the ridges in Plate 16.3F being especially interesting.

The cells between the ridges are also of interest since the epicuticular waxes, with which they are coated, are so clearly structured. These cells are unlikely to experience direct abrasion and yet, if the waxes from the W_1 plants in Plate 16.4A are compared with those from the W_2 plants in Plate 16.4B, the greater aggregation in the latter treatment is clearly apparent. This comparative aggregation of the waxes may be seen at a higher magnification in the corresponding Plates 16.4C and 16.4D. By contrast, the cells on the ridges of the adaxial surfaces

Plate 16.3

Scanning electron micrographs of the surfaces of laminae of S.170 *Festuca arundinacea* Schreb.

A. The abaxial surface from a W_1 plant (X 80)

B. The abaxial surface from a W_2 plant in an area of surface abrasion (X 80)

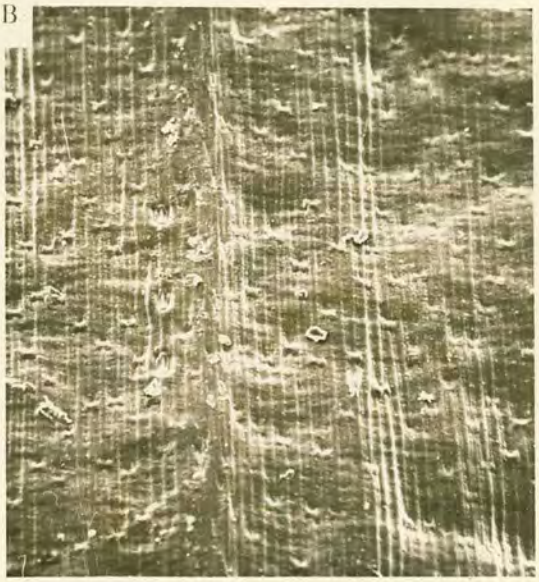
C. The adaxial surface from a W_1 plant (X 80)

D. The adaxial surface from a W_2 plant in an area of surface abrasion (X 80)

E. The adaxial surface from a W_2 plant showing an enlargement of the damage occurring between the ridges shown in D (X 380)

F. The adaxial surface from a W_2 plant showing an enlargement of the damage occurring on the ridges shown in D (X 390)


A


B


C


D


E


F

Plate 16.4

Scanning electron micrographs of the surfaces of laminae of S.170 *Festuca arundinacea* Schreb.

A. The adaxial surface from a W_1 plant showing the cells between the ridges (X 680)

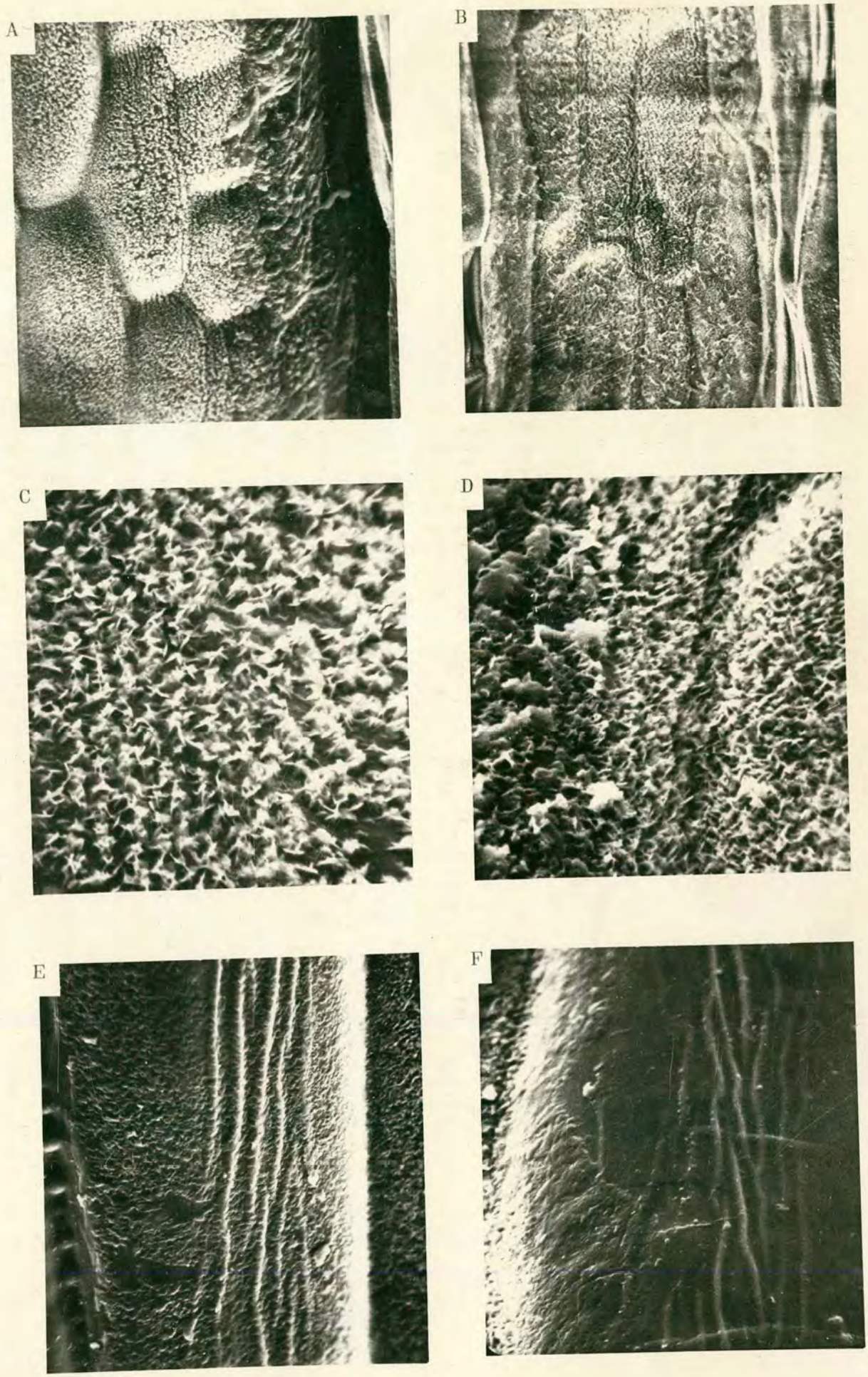
B. The adaxial surface from a W_2 plant showing the cells between the ridges (X 650)

C. The adaxial surface from a W_1 plant showing the epicuticular wax structures of the cells in A (X 4000)

D The adaxial surface from a W_2 plant showing the epicuticular wax structures of the cells in B (X 3700)

E. The adaxial surface from a W_1 plant showing the epicuticular wax structures on the cells on the ridges of Plate 1C (X 1600)

F. The adaxial surface from a W_2 plant showing the epicuticular wax structures of the cells on the ridges of Plate 1D (X 1500)


A
B
C
D
E
F

have epicuticular wax coatings that are much more variable both in form and distribution. Plates 16.4E and 16.4F show W_1 and W_2 surfaces respectively. Where there is such variability, the assessment of wind damage is more difficult, but Plate 16.4F does seem to show the effects of surface rubbing especially as the material itself is a magnification of that shown in Plate 16.3D. A further point of interest is that the cells shown in Plate 16.4A seem to have a much greater curvature than those shown in Plate 16.4B. This may be due to a higher turgidity in the cells of the W_1 leaves, perhaps reflecting the higher diffusion resistances shown by Grace (1974).

Having gained an insight into the nature of the abrasion marks, it would be useful to have some way of quantifying them. Here the problem is much more complex than with the fracture lines as they vary in severity and it may require the use of a microscope to determine the full extent of the damage. Also, it is quite possible that in plants exposed to wind, wax abrasion may occur in areas that are not obviously damaged. This may be expected if contacts between leaves occur only occasionally. Plates 16.4A and 16.4B show that the structures of the waxes may become altered, even if the cells themselves have not been in contact with others. In view of this, perhaps an indirect approach such as the measurement of diffusion resistance or transpiration rate at night might be of use.

One means which might be feasible is the measurement of leakage of ions from wind damaged leaves. This could be done by monitoring changes in the conductivity of solutions in which damaged and undamaged leaves were immersed. This method has been used by Matthews and Bradnock (1968) in field emergence studies of peas and French beans. Peas which had higher rates of leakage, reflecting membrane damage, were found to have lower germination rates. Polwarth (1970) has also used this approach to measure frost damage in Vaccinium and he found that increases in conduc-

tivity reflected increased frost damage. Membrane permeability has been comprehensively reviewed by Simon (1974) and he suggested that droughted tissues may leak in the period during rehydration. It therefore seems likely that wind might produce an increase in leakage and it would be interesting to investigate this aspect further.

A crucial point with abrasion damage is to know how long after a period of wind exposure such effects may be expected to last. The evidence from other species is varied; most bloomed plants have some ability to recover from mechanical damage whilst the leaves are still growing. This has been noted in Chrysanthemum segetum and Eucalyptus species,an exception being peas, which hardly recover at all (Martin and Juniper, 1970). This aspect in F. arundinacea requires further experimentation.

16.4 Conclusions

It can be concluded from this evaluation of mechanical damage that the reductions in rates of photosynthesis and lower diffusion resistances found by Grace and Thomspon (1973) may, in part, be due to this effect. The crucial point here is to be able to correlate the incidence of mechanical damage and the reduction in diffusion resistance or increase in water loss and then to assess how long such effects may last.

SECTION 6.

MECHANISMS OF ACTION OF WIND AND THE AGRICULTURAL SIGNIFICANCE OF ITS EFFECTS

CHAPTER 17.

THE MECHANISMS OF WIND ACTION

17.1 Introduction

The purpose of this chapter is to consider how the experimental work described in previous chapters contributes to the general understanding of how wind affects the growth of plants.

In discussing the mechanism of wind action, a division can be made into those effects due to the motion of the plants and those due to the motion of the air, although there is some overlap between them.

17.2 The effects of plant motion

The motion of plants themselves may have marked effects on growth. This aspect was investigated by Kahl (1951) with experiments on shaking plants, an effect analogous to wind action. She found that in lettuce, transpiration and respiration were increased and assimilation was inhibited. These effects were believed to result from structural changes within the cells.

More recently, Neel and Harris (1971) shook the trunks of 8 plants of Liquidambar styraciflua for 30 seconds daily for 27 days and compared the growth with 8 unshaken controls. Shaking reduced height growth by 70-80% and also caused the formation of terminal buds in 6 out of the 8 trees so treated. There were significant reductions in the number of nodes and lateral branches formed and also the length of internodes, but significant increases in the length and diameter of the vessel members and the length of the wood fibres. They also found that manual manipulation of cocklebur leaves for a few seconds a day caused a 30% reduction in growth and earlier senescence. They suggested that a growth hormone was implicated in these responses.

Turgeon and Webb (1971) carried out a similar experiment with Cucurbita melopepo in which they shook the petioles for 30 seconds daily for 20 days and lightly stroked the leaf blades. Lengths of petioles and fresh weights were significantly reduced and there was an increase in radial growth in the petioles. They suggested that these growth responses could occur as a result of ethylene produced by the mechanical stress since ethylene is known to stimulate radial growth in epicotyls.

Parkhurst and Pearman (1972) pointed out that certain corollary evidence produced by Neel and Harris (1971) could be explained by means other than hormonal and suggested that cavitation, leading to a water stress, could be an alternative explanation.

The idea of cavitation was rejected by Neel and Harris (1972), who pointed out that they had obtained reductions of 5% in height growth, 30% in leaf numbers and 15% in leaf length with daily shaking of Zea mays. The growth rate of those plants, when subsequently left undisturbed, returned to that of the controls within 3 days. They too suggested that ethylene might be involved.

Other reductions in growth have been reported by Jaffe (1973) who referred to the growth responses from mechanical stimulation as thigmomorphogenesis. He found that, whilst there was considerable variation between species, simple gentle rubbing produced a considerable decrease in elongation in many plants. Also, the mechanical stimulus affected aspects of growth and development other than stem elongation such as the growth of tendrils, leaves and petioles. He also noted that whilst the response to rubbing was immediate, the plants slowly recovered over a period of several days. He suggested that these responses represented an adaptation designed to protect plants from exposure to high winds and also that ethylene might be involved as a causal mechanism.

Hiron and Wright (1973) reported that by blowing warm air on to a bean plant, the plant first wilted and then recovered turgidity. Associated with this was an increased level of abscisic acid in the leaves. They suggested that this induced stomatal closure and thus restored turgidity. It seems likely that this situation is analogous to the shaking experiments as it is probable that the leaves were in motion. The shaking experiments, implying that ethylene was involved, made no mention of any attempt to measure it.

17.3 Mechanical damage

Another result of the motion of plants is the occurrence of mechanical damage. These effects in Festuca arundinacea have already been described in detail in Chapter 16 and, in the literature, there have been other cases cited but not so deeply examined. There have also been a series of papers dealing with damage induced by wind-blown particles (Poole, 1933/34; Lyles and Woodruff, 1960; Skidmore, 1966; Fryrear, 1971; Fryrear, Stubbendieck and McCully, 1973), where it is often difficult to determine the precise role played by wind.

There is also the possibility of increased susceptibility to fungal infections of plants damaged by wind. Sill et al. (1954) suggested that the transmission of the wheat streak-mosaic virus was aided by abrasive leaf contacts during strong winds. Plate 16.3F illustrates clearly how such an infection could occur, especially in cells that have been torn wide open.

From Chapter 16, it was concluded that damage may occur through motion by itself or through abrasive leaf contacts. The extent to which these effects occur in other species is largely unknown and it would be very interesting to carry out further comparative studies. The type of damage which occurs seems likely to vary considerably. In conifers with

short needles, where the main motion due to wind is by whole branches, the opportunities for abrasive contacts would be limited. In pines, especially those with longer needles, this factor would increase. In broad-leaved trees, there may be marked effects of leaf flutter, in addition to a greater opportunity for physical contact. Leaf flutter seems to act in a similar manner as in tatter flags and in extreme situations may lead to considerable loss of leaf area. This effect is likely to be exacerbated in young leaves, where structural tissues are not fully developed. In crop plants, there are also likely to be marked differences depending on the type of leaf and also the way in which the crop is grown. For example, more opportunities for physical contact between leaves are likely to occur in crops where canopy closure is the norm than where plants are grown further apart.

17.4 The penetration of radiation into the canopy

Another aspect, which is probably affected by leaf movement, is the penetration of radiation into the canopy. There have been a number of studies in which the penetration of radiation into leaf canopies has been examined in relation to leaf angle e.g. Loomis, Williams, Duncan, Dovrat and Nunez (1968). In general, these studies report greater penetration of radiation at higher leaf angles. Loomis, Williams and Duncan (1967) and Loomis, Williams and Hall (1971) have suggested that when growing crops at high densities, the selection of a variety with more erect leaves may be beneficial, especially under high levels of irradiance.

In the wind tunnel yield experiments, the angles of the leaves were altered and became more parallel to the soil surface under the W_2 conditions. In windy situations, the applicability of plant production models incorporating sophisticated descriptions of canopy architecture is therefore open to serious question.

Apart from the overall penetration of radiation into leaf canopies, leaf movement also affects the penetration of flecks of sunlight. This factor was investigated by McCree and Loomis (1969), but more in relation to the passage of clouds rather than to the effects of wind. However, some of the fluctuations were quite rapid. In experiments with Cucumis sativus using fluctuation frequencies of 10^{-2} - 10^{3} sec., the mean photosynthetic rate i alternating light was always within a few per cent of the mean of the 2 original photosynthetic rates under steady conditions.

Kriedemann, Törökfalvy and Smart (1973) examined the effect of sunflecks on grape vine leaves. They found no consistent relationship between the frequency of sunfleck occurrence and windspeed, but the average results indicated a mean duration of sunflecks of 0.6s and an intervening low radiation period of 1.2s. They noted that Ino (1970) had found similar periodicities under Betula platyphylla and Cinnamonum camphora. Kriedemann, Törökfalvy and Smart suggested that sunflecks were likely to be of little significance for production at the high light intensities experienced at the tops of canopies, but might be of value where lower levels of radiation are experienced deep in the canopy.

Desjardin, Sinclair and Lemon (1973) concluded that short-term light fluctuations in maize would have little or no effect on the photosynthetic activity of a crop grown in the field. However, they carried out no simultaneous measurements of photosynthesis.

In the wind tunnel yield experiments, the level of irradiance was quite low. Also, being from fluorescent tubes, it was entirely diffuse and so there would have been no situation analogous to sunflecks. The canopy heights by the final harvests usually varied between 15 cm and 25 cm and the leaf area indices were low. In the $W_1P_2N_2$ and $W_2P_2N_2$ treatments in yield experiment 4, the values were 3.53 and 2.91 respectively.

It would, therefore, seem likely that, although there may have been some reduction in the penetration of radiation to the bottom of the canopy due to the alteration of leaf angle, the effect on the growth of the sward would probably have been small.

17.5 Water relations

There has probably been more experimental work on this aspect of wind action than on any other. The work in this thesis has not been directly concerned with these effects, except as a consequence of mechanical damage and as a possible reason for the reduced rates of photosynthesis, found in Chapter 15. This thesis can perhaps be regarded as paving the way for further studies in this field.

In the yield experiments, soil moisture was always kept non-limiting to minimize the possibility of water deficits. However, Grace and Thompson (1973) (Appendix 1) showed that despite this, the mean relative saturation deficits of the wind-exposed plants were higher.

In the literature, there have been many reports of increased rates of transpiration due to wind (Caldwell, 1970a and 1970b; Gäumann, 1942/43; Gäumann and Jaag, 1939a and 1939b; Hygen, 1951 and 1954; Martin and Clements, 1935; Satoo, 1948a, 1948b, 1948c, 1949, 1953 and 1955b; Tranquillini, 1969 and 1970; Wrenger, 1935/36). There have also been examples of reductions in transpiration such as in Rhododendron ferrugineum (Caldwell, 1970a and 1970b; Tranquillini, 1969 and 1970). Many of the increases in transpiration were initial effects, usually followed by a decrease, sometimes to levels below the initial rates, due to stomatal closure. In species such as R. ferrugineum, the stomata seem to close very rapidly and may respond to shaking rather than a water deficit. This would suggest a similar response to that reported by Hiron and Wright (1973), where they suggested that abscisic acid might be involved.

The reason for the increases in transpiration has usually been considered to be the reduction of the boundary layer. The work by Grace and Thompson (1973) using model tillers shows that such effects in F. arundinacea are not likely to be important except at very low windspeeds. In plants with large leaves, the situation may be quite different due to the existence of much thicker boundary layers. Also there may be differences due to the levels of turbulence. A study of the boundary-layer resistance of still and flapping leaves was undertaken by Parlange, Waggoner and Heichel (1971). They examined the effects of laminar and turbulent air flows on the boundary layer and found that compared to a steady laminar flow, the turbulence of a realistic wind decreased resistance by a factor of about 2.5. This factor seemed to be constant whether a leaf was flapping or not. The evidence would suggest, therefore, that there is much research to be done on leaves of different shapes in relation to water loss.

In addition to aspects which might affect gaseous diffusion, there is also the possibility of more active mechanisms produced by wind. Netolitzky (1926) considered that in wind-exposed leaves, gas exchange would be facilitated by suction effects through the stomata, although he was more concerned with carbon dioxide.

Woolley (1961) also examined some of the means by which wind could increase gas exchange, but from the viewpoint of transpiration. These were the decrease in air pressure on the lee-side of a leaf, the ventilation of intercellular spaces caused by the actual passage of air through amphistomatous leaves and the bending of the leaves in the wind causing a pumping of air out of the stomata. He calculated that none of these mechanisms could account for as much as 1% of the transpiration of maize leaves. He verified the pumping aspect experimentally and found that the difference in transpiration was less than 3%.

Despite these conclusions, it may well be worth further exploration of the pumping effect experimentally. The arrangement of the guard cells in the Gramineae is different from that in other families and it would be interesting to simulate the possible pumping action of leaves in a dicotyledon.

One aspect, which would be very interesting to know, is whether the yield effects shown by exposing the plants to wind in the day, would also occur if the plants were exposed at night. In this case, the stomata would be expected to be closed and water loss considerably reduced. Here, the indication of the reduced leaf resistance in the wind-exposed plants by Grace and Thompson (1973), due to abrasive leaf contacts, is of significance. Recent work by Grace (1974) has shown that the transpiration rate of F. arundinacea is increased at night by exposure to windspeeds of 3.5m s^{-1}, associated with a reduction in cuticular diffusion resistance. Festuca pratensis, Lolium multiflorum and Dactylis glomerata all showed similar effects.

17.6 Leaf temperatures

The effects of wind on leaf temperature are primarily due to alterations in the thickness of the boundary layer and, consequently, the efficiency of convective heat exchange. The thickness of the boundary layer is otherwise determined by the leaf size, its surface structure and its shape.

Wuenscher (1970) examined the effect of shaving the hairs of leaves of Verbascum thapsus on the thickness of the boundary layer. He found that leaves with hairs were warmer due to a thicker boundary layer.

Vogel (1970) examined the effect of low windspeeds on the convective cooling of copper plates of different shapes. Two of the plates represented the sun and shade leaves of Quercus alba. He found that a circular plate dissipated less heat than the more irregular shapes. Also, even

very slight air movements caused considerable dissipation of heat, but this effect was very dependent on the orientation of the plates, especially those of more regular shape.

Casperson (1957) compared the leaf temperatures of Avena sativa, Hydrangea opuloides, Kalanchöe blossfeldiana and Echeveria peacockii, when exposed to a wind of 0.7m s^{-1}. The temperatures of all 4 leaves rose when under lights, but that of A. sativa, being the narrowest leaf, fell to a level closest to ambient when exposed to wind.

The effects of wind on leaf temperatures of F. arundinacea would therefore have been unlikely to have been large and this was confirmed by measurement. In this case, not only were the leaves small, but the W_1 windspeed in itself would probably have been sufficient to dissipate any minor heating effects that might have occurred.

There are two other points of interest here. Firstly, the effect of turbulence causing winds from different directions to flow over leaves may be significant in itself. Secondly, in situations where wind is strong enough to cause leaf tearing, the boundary layer characteristics of a torn leaf will be permanently altered and the temperatures experienced will be closer to ambient throughout the remaining life of the leaf.

17.7 Discussion and conclusion

Most of the literature and also the experimental work in this thesis has emphasised that, except at low speeds, wind is likely to be adverse to plant growth. The object of shelterbelts and windbreaks is to reduce wind and so ameliorate such adverse effects. In view of the difficulties in establishing and maintaining such structures, it is pertinent to consider whether this is the only approach available. As an alternative, should the possibilities of producing windproof plants be explored?

The idea of the responses of plants to wind as being a reflection

of phenotypic plasticity was a continuing theme in the experiments by Whitehead. Bradshaw (1965) has discussed the significance of this concept at length and cites many examples of plants or plant organs exhibiting plasticity towards different environmental factors.

The results of the yield experiments in this thesis can also be interpreted in terms of the plasticity of the responses to the experimental treatments; nitrogen and to a lesser extent phosphorus, both tend to have greater effects than wind.

Allard and Bradshaw (1964) have discussed the significance of plasticity in plant breeding and drawn attention to the conflict between the expression of plasticity and the agronomic need to maintain high and consistent performances from crop plants. In the practical context of this study, the slow growth of grass in spring may be partly an expression of phenotypic plasticity. Thus, in order to increase early bite and to maintain production despite wind, the reduction of phenotypic plasticity would be of agronomic advantage.

If the plasticity of response to wind is related to water loss, the means by which this could be reduced should perhaps be explored. One possibility is the use of plants with thicker cuticles or with pronounced blooms in windyareas, but there is no indication that this has yet been considered for crop plants by plant breeders.

If this approach is not practically feasible, the use of film anti-transpirants could be considered particularly for crops of high economic value. For full effectiveness, applications would have to be made in relation to the previous wind exposure. As mentioned previously, the significance of physical damage cannot be fully assessed until the duration of the effects can be determined. This would seem to be a very useful line for further research.

There is now a considerable amount of information on how the yields of plants may be affected by the action of wind, either in isolation or in relation to water supply. There is, however, considerable scope for further research into the mechanisms of wind action.

In natural situations, wind rarely acts in isolation from other factors and the interactions with the availability of nutrients demonstrated in the wind tunnel yield experiments are clear examples. Such interactions may well not be confined to edaphic factors; the effects of atmospheric pollutants such as sulphur dioxide, exhaust fumes from vehicles and even salt spray may be much exacerbated in combination with wind. The controlled environment wind tunnel is an excellent tool for such investigations and clearly, the scope is very wide.

A major difficulty exists with wind tunnel experiments in the use of plants not previously subjected to wind, since there may be responses to the initial exposure, which are quite different from, or which much exaggerate the responses likely in the field. It would seem wise to either experiment on plants that have been previously exposed to wind for a long period or to establish the relationships between wind-treated and un-treated plants. Most of the practical situations involve plants exposed to wind for long periods and, if experiments are to retain their relevance, long-term experiments ought to be undertaken, despite the considerable problems in execution.

Ideally, a wind tunnel, with at least 4 parallel working sections in which windspeed may be controlled independently of other factors, is required for such studies. The controlled environment wind tunnel at Edinburgh has demonstrated that, in principle, an aerodynamically-sound wind tunnel may be combined with good control of environmental conditions. A larger version would surely not be a technical impossibility.

CHAPTER 18.

THE AGRICULTURAL SIGNIFICANCE OF THE STUDIES ON FESTUCA ARUNDINACEA

The previous Chapter, in considering some of the wider questions that might be asked in future studies on wind, tended to move away from the original theme of this thesis, i.e. how the use of shelter might be expected to affect the early regrowth of grass in spring. It is, therefore, of relevance to consider the extent to which the experiments in this thesis have contributed to an understanding of this problem.

The field experiments indicated, although inconclusively, that increases in yield could be expected from shelter in spring. This particularly applied to shelter from the east or the west when nutrient supplies were adequate. It would be unwise to draw firm conclusions for agricultural policy from such work, but the extension of this situation into the controlled environment of the wind tunnel, is of greater consequence. The crucial point here is the feasibility with which wind tunnel results may be translated to shelter situations in the field.

The wind tunnel yield experiments indicated two situations in which the beneficial effects of shelter or the reduction of wind are likely to be most pronounced. These are in conditions of high nutrient availability and where moisture tends to be limiting in spring. Translated to particular areas, this would mean farms practising more intensive agriculture in the east of Scotland. This would confirm the observation by Marshall (1967) in his literature review that most of the responses to shelter have been reported from the drier areas of the world. One wonders also, if this combination of factors does not already exist where there is particular strong emphasis on the use of shelter such as the Cockburn and Cockdurno Farms, Balerno, Midlothian.

This also has further significance for farms contemplating intensifying production. The wind tunnel experiments indicated that whilst a response to wind may be apparent only under conditions of high nutrient availability, the converse also applies, i.e. that maximum responses to application of fertilizer are only likely to be felt in areas where wind is reduced. Horticultural crops tend to be grown in more fertile soils and this may be one reason why they tend to show greater responses to shelter. At a time of rapidly rising costs of fertilizers, an increase in efficiency due to shelter would clearly be advantageous.

It is therefore recommended that if any more practically based trials of shelter effects on spring production are contemplated, they should be carried out in the east of Scotland and on farms using high levels of fertilizers, especially nitrogen.

Perhaps some parallels can be drawn here with the effects of wind on grass and the incidence of winter burn and winter kill. These were very widely reported phenomena in the spring of 1969, when cold conditions, especially in February, followed a mild January. This prompted the "Study Conference on Winter Kill" at Auchincruive in July of that year. Herriott (1969) stated that this was a phenomenum really only applying to farmers using above 200 units of nitrogen a year, and this comment seemed to find general acceptance. Perhaps 200 units of nitrogen could also be used as a guideline in identifying areas likely to gain from shelter, but this must be regarded as being somewhat speculative. The connections between winter burn, winter kill and shelter are an area that would perhaps merit further experimental investigation. The situation believed to be instrumental in high incidences of winter kill is where a warm wind passes over a cold soil, thereby inducing a physiological drought in the plants. The controlled environment wind tunnel would provide a very useful means for undertaking such a study, provided a system for controlling root

temperature could be developed.

In the practical context of these experiments, mention must be made of the applicability of measurements on tall fescue to the likely performances of other species. The most widely used species in intensive agricultural situations in Scotland is perennial ryegrass. There was an indication in the field experiments that the response to shelter was more pronounced in ryegrass. Grace (1974) examined the transpiration of tall fescue, meadow fescue, Italian ryegrass and cocksfoot and found similar patterns in water loss at night, suggesting that all species were experiencing abrasion damage. Whether this experiment can be extrapolated to the effects on yields in the field is speculative, but at least there is no indication of a contradictory situation occurring.

Although it is not the purpose of this thesis to champion the use of tall fescue, it does have advantages as an experimental material. Its advantages in early production are also widely accepted. The problems of early establishment seem to have blighted the prospects for extensive use of this species, but it should be noted that Kentucky 31 tall fescue, a very widely used forage and amenity grass in the U.S.A., does not have these difficulties. This variety is also well-known for its tolerance of a wide range of adverse environmental conditions.

The investigations on mechanical damage in themselves may also have significance for field conditions, but the crucial point is to know for how long such effects might last. Clearly, if leaves are torn, the damage must be permanent, but the duration of the more subtle abrasion damage is less certain. In both cases,not only will shelter itself be important, but also the direction of shelter. Plants normally sheltered from one direction might suffer mechanical injury due to a sudden gale from another direction. Leaves would then have modified boundary layers and be pre-

disposed to increased water loss for the rest of the growing season.

In conclusion, it is considered that if one is prepared to translate the results obtained in the controlled environment wind tunnel to the field, then the control of wind effects on plants should help to increase early spring production, especially in areas of more intensive agriculture in eastern Scotland.

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APPENDIX 1.

THE AFTER-EFFECT OF WIND ON THE PHOTOSYNTHESIS AND TRANSPIRATION OF *FESTUCA ARUNDINACEA*

By

J. Grace and J. R. Thompson

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The After-effect of Wind on the Photosynthesis and Transpiration of *Festuca arundinacea*

By

J. GRACE and J. R. THOMPSON[1]

Department of Forestry and Natural Resources, University of Edinburgh, EH9 3JU, U.K.

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Abstract

The after-effect of wind on photosynthesis and transpiration of *Festuca arundinacea* Schreb. was determined. Following a period of exposure in a controlled environment wind tunnel the wind-treated plants showed reduced rates of photosynthesis when compared with the controls under standard conditions. Evaporation from paper model tillers was measured and the boundary layer resistance was shown to be low in all but very low wind speeds. Analysis of CO_2 and H_2O diffusion pathways indicated that mesophyll resistance in wind-treated plants was higher whilst leaf surface resistance was lower than in the controls. The high mesophyll resistance in the wind-treated plants was attributed to reduced water content.

Introduction

It has long been the practice in windy regions to construct walls, screens or rows of trees to locally reduce the windspeed in the hope of increasing the yield of nearby crops (Caborn 1965). Because of the large capital outlay and the uncertain effects of such practices, agriculturalists and foresters have often used experimental windbreaks in an attempt to evaluate the biological and economic returns. Yield increases of between 5 and 300 % have been found in a variety of crops thus sheltered (Hogg 1962, Lines 1962) but reductions in yield are also not uncommon (Hogg 1962).

Shelter may affect the microclimate of an area in a variety of ways, reduction in windspeed usually being considered to be the most important. Some insight into the effects of altering windspeed has been obtained from the measurement and analysis of plant growth under laboratory or glasshouse conditions in which windspeed has been varied independently of other environmental parameters. Reviewing the literature on this subject, Wadsworth (1964) noted that there appears to be an optimum windspeed for plant growth. At very low windspeeds assimilation rate was thought to be limited by the resistance to gaseous diffusion between the ambient air and the leaf surface, whereas at higher speeds, 1–15 m s^{-1}, the assimilation rate, as measured by growth analysis techniques, was much depressed. This reduction has been attributed to leaf water deficits resulting from transpiration rates exceeding rates of water uptake since there is some evidence that this may be ameliorated by increasing the water supply to the roots (Satoo 1948, Whitehead 1963).

The present experiment is part of a larger investigation designed to examine some of the effects of wind on the growth of grass in upland Britain. By use of a controlled environment wind tunnel values of windspeed, temperature, humidity and radiation were adjusted to realistically represent conditions prevailing during spring in the Scottish Southern Uplands. Photosynthesis and transpiration of *Festuca arundinacea* were measured in standard conditions after a period of wind treatment.

Experimental Procedure

Plant culture

Seeds of tall fescue, *Festuca arundinacea* Schreb., strain S.170 were germinated in trays containing a peat/fine sand compost. At 2 weeks, when seedlings were 5 cm high, they were planted into boxes 28 cm × 20 cm × 15 cm deep, using a 5 cm square spacing. The soil medium was a peat/sand mixture based on the U.C. mix 1D of Matkin and Chandler (1957), phosphorus being applied in the form of 45 mg/l of di-sodium hydrogen orthophosphate and supplemented by 600 mg/l of ammonium nitrate.

[1] Current address: Department of Botany and Plant Technology, Imperial College of Science and Technology, London. U.K.

When the plants had reached a standard size (3–4 tillers), they were removed from the glasshouse and stored in a cold room at 10°C with a 12 h photoperiod. To simulate the effect of mild grazing, the plants were trimmed to 8 cm after a week, and the temperature was thenceforth kept at 6°C. After 6 weeks the plants were placed in the wind tunnel (T.E.M. Engineering).

Wind treatment

In the wind tunnel the plants were subjected to an air temperature of 5±0.5°C, a relative humidity of 80±2 %, and an irradiance of 6.02 mW cm^{-2}. The light source consisted of a bank of 21 Thorn White Amalgam and 3 Radar Red fluorescent tubes.

Windspeed above the swards was adjusted to produce 3.5 m s^{-1} for the wind-treated plants, and 1 m s^{-1} for the controls, and was measured by a mini-vane anemometer (Schiltknecht). Turbulence was 17 % in the wind-treated plants and 29 % in the case of the controls.

The leaf temperature of both the wind-treatment and the controls, as measured by copper-constantan thermocouples constructed with wires of diameter 0.10 mm, rose to not more than 0.5°C above ambient air.

Both sets of plants were placed in a growth cabinet at 5±0.5°C and 75 % relative humidity during their 12 h dark period. Soil moisture was maintained at a high level by watering to field capacity at the earliest indication of surface dryness.

Photosynthesis and transpiration

To measure photosynthesis and transpiration, boxes of grass were removed from the wind tunnel at intervals of 2, 5, 7, and 9 days, and placed in a small controlled environment growth cabinet (Controlled Environments Ltd.) in which whole tillers, still rooted, were sealed into a cylindrical clear perspex cuvette for measurement of photosynthesis and transpiration rates.

An airstream, taken from outside the building, and with a carbon dioxide concentration of 320±20 µl/l was drawn through distilled water at 3.4±0.1°C so that the airstream became saturated at that temperature. The airstream was then pumped via a flowmeter (G. A. Platon Ltd.) through the cuvette (1.2 l min^{-1}) and then to waste. Small airstreams left the main one immediately before and after the cuvette, and were directed to a thermocouple psychrometer unit (Slatyer and Bierhuizen 1964) and then to a train of drying towers before passing to a Grubb Parsons SB2 infra-red gas analyser. Photosynthesis and transpiration were therefore measured from a knowledge of the CO_2 and H_2O content of the inlet and exhaust gases and of the air flow rate through the cuvette.

All measurements were made at a leaf temperature of 14.5±0.5°C and a leaf/air water vapour pressure difference of 6.5±0.5 mbar.

The light source in the cabinet was a bank of 8 Sylvania V.H.O. cool white fluorescent tubes with 4 incandescent lamps. The walls of the cabinet are reflective so that the plants were irradiated with a diffuse light field resembling a standard overcast sky (Grace 1971). To vary irradiance half of the lamps could be turned off, and a screen of black mesh could be inserted into a slot underneath the lamps. Irradiance was measured with a Kipp solarimeter horizontally placed at the height of the base of the tillers.

The gas analyser was calibrated and used as a differential analyser by mixing a CO_2-free airstream at low flow rates with the atmospheric stream which had first passed through the reference cell of the analyser. The diluted stream was directed to the second cell. Airstreams were stabilised by appropriate Flostats (G. A. Platon Ltd.) and the flow rate of the CO_2-free airstream was measured accurately with a soap-bubble flowmeter (Levy 1964).

Leaf water content

3–5 cm segments were cut from leaf blades chosen at random. They were weighed immediately (fresh weight) and again after standing in distilled water for 24 h at 15°C in the dark (turgid weight). The segments were taken at the end of each photoperiod, and over a period of 6 days, corresponding to the time interval between watering the boxes. Water content was expressed as relative saturation deficit (RSD).

$$\text{RSD} = \frac{\text{turgid weight} - \text{fresh weight}}{\text{turgid weight}} \times 100\ \%$$

Results

The general relationship between photosynthesis and irradiance for wind-treated and control plants is given in Figure 1. The maximum rate of net photosynthesis found in the controls is 1.6 µl CO_2 cm^{-2} min^{-1}. This falls within the limits obtained for many crop plants (Gaastra 1959) and is close to values obtained for other grasses, for example *Dactylis glomerata* (Hesketh and Moss 1963), *Lolium perenne* (Woledge 1972), wheat (Khan and Tsunoda 1970) and barley (Dale and Felippe 1972). It is however far higher than the rates reported for the same strain of *F. arundinacea* by Jewiss and Woledge (1967). Their low rates (0.15–0.5 µl CO_2 cm^{-2} min^{-1}) may be attributed to the relatively low irradiance they used, 5–8 mW cm^{-2}, which according to our Figure 1 is well below the light-saturation point, and would result in rates between 0.48 and 0.6 µl CO_2 cm^{-2} min^{-1}.

The wind-treated plants showed a reduction in net photosynthesis at high irradiance. This difference was not due to an increase in dark respiration, which did not differ significantly from the controls, nor may it

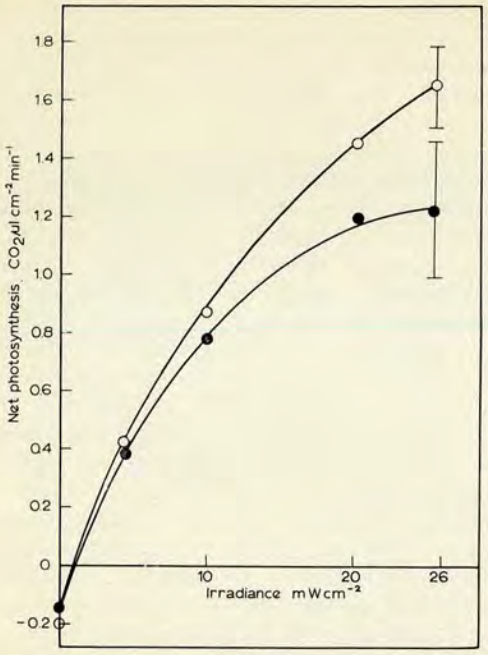

Figure 1. *Net photosynthesis of wind-treated* (●), *and control plants* (○), *of Festuca arundinacea at different levels of irradiance measured per unit leaf area under standard conditions.* Points are the means of 13 measurements, vertical bars represent 95 % confidence limits. Wind treatment lasted 2–9 days.

be attributed to differences in the leaf area/leaf dry weight ratio which was unaltered by wind treatment.

Light saturation occurred at 20 mW cm^{-2} in the case of the wind-treated plants, but in the case of the controls it did not occur, even at the highest irradiance used. There is an indication that the initial slope of the light-response curve may be shallower in the case of the wind-treated plants.

Photosynthesis was measured after 2, 5, 7, and 9 days of wind treatment, but since the results obtained on these occasions were not statistically significantly different from each other, Figure 1 consists of the pooled data from 26 plants. There was however a trend in the data (% of controls) towards recovery, the effect of wind treatment being most pronounced after 2 days and least after 9 days in the wind tunnel (see table below).

Time, days	2	5	7	9
Net photosynthesis, %	47	62	82	84

Transpiration rate was measured simultaneously with photosynthesis, and the pooled data is given in Figure 2. Even though the leaf/air vapour pressure gradient and ventilation conditions were the same in both cases, the wind-treated plants more frequently transpired at the higher rates and less frequently at rates less than 0.6 µg

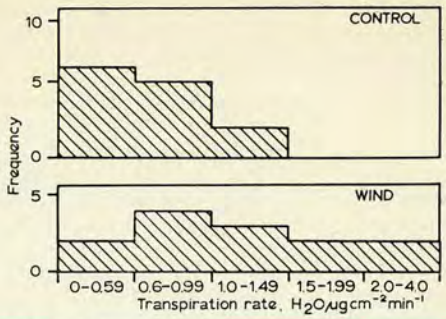

Figure 2. *Frequency distribution of transpiration rates of Festuca arundinacea measured under standard conditions.* Upper; controls. Lower; wind-treated plants. All measurements at 26 mW cm^{-2}.

H_2O cm^{-2} min^{-1}. The probability of the frequency distributions differing to this extent by chance alone may be assessed by using the χ^2 test, provided that the three highest transpiration classes are combined so that no class is represented by a frequency of less than 1 (Snedecor and Cochran 1967). The resulting $\chi^2 = 11.85$, d.f. = 2, $p = 0.005$, indicates a real difference in the frequency distributions of transpiration rate between the wind-treated and control plants.

To account for the observed differences in net photosynthesis an analysis of the H_2O and CO_2 diffusion paths was made by the method of Gaastra (1959). Implicit in this method is the idea that the rate of photosynthesis at saturating irradiance is limited by the inward diffusion of CO_2 from the ambient air to the carboxylation sites which occurs through a chain of three diffusive resistances, the first, r_a, at the boundary layer above the leaf, the second r_l at the leaf surface including the stomatal apparatus and cuticle, and the third, r_m within the mesophyll. This method has fallen into some disrepute recently since it has been indicated (Woolhouse 1967–1968, Björkman 1968) that in some species at least, the rates of photosynthesis are limited instead by the concentrations of carboxylating enzymes present in the leaf. For a recent critique of Gaastra (1959) the reader is referred to Jarvis (1971).

The boundary-layer resistance, $r_a{}^{H_2O}$, was calculated from the evaporation rate q_v of water from a paper model of a tiller

$$r_a{}^{H_2O} = \frac{C_1 - C_2}{q_v}$$

where C_1 and C_2 are the water vapour concentrations at the liquid-air interface and in the ambient air respectively. In F. arundinacea the stomata are mostly confined to the adaxial surface and so the model consisted of aluminium foil blades with wet filter paper glued to one side only. A thermocouple was fixed to a single "leaf" and the model was inserted into the cuvette just

Table 1. *Aerodynamic resistance $r_a^{CO_2}$, leaf resistance $r_l^{CO_2}$, and mesophyll resistance $r_m^{CO_2}$ for wind-treated and control plants of Festuca arundinacea under standard conditions.* Units; s cm^{-1}.

Treatment	$r_a CO_2$	$r_l CO_2$	$r_m CO_2$
Wind	1.26	2.58 ± 2.2	8.18 ± 0.18
Control	1.26	5.36 ± 2.9	2.41 ± 0.12

as the real tillers had been, evaporation rate being measured under a variety of conditions of air flow through the chamber.

The leaf resistance $r_l^{H_2O}$ was calculated from the transpiration rate q_v of real tillers

$$r_l^{H_2O} = \frac{C_1 - C_2}{q_v} - r_a^{H_2O}$$

The mesophyll resistance r_m was calculated by subtracting $r_a^{H_2O}$ and $r_l^{H_2O}$ from the total resistance

$$r_m^{CO_2} = \Sigma r^{CO_2} - (r_l^{H_2O} + r_a^{H_2O}) \left(\frac{D_{H_2O}}{D_{CO_2}}\right)$$

The ratio of the diffusion coefficients of H_2O and CO_2 in air, D_{H_2O}/D_{CO_2} was taken as 1.57 (Meidner and Mansfield 1968), and the total resistance, Σr^{CO_2} is calculated from the net photosynthetic rate F, the respiratory efflux of CO_2 in the dark R, and the concentration of CO_2 in the ambient air and at the carboxylation sites, C_a and C_c respectively.

$$r^{CO_2} = \frac{C_a - C_c}{F + R}$$

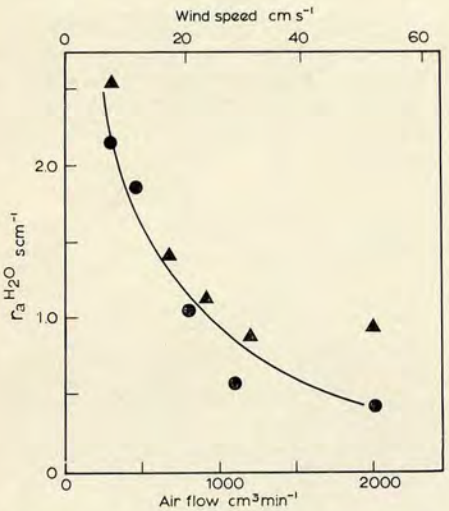

Figure 3. *Boundary layer resistance, $r_a^{H_2O}$, for tiller-shaped filter paper with either flat (●), or folded blades (▲).*

C_c was assumed to be 55 µl/l, a figure obtained by Wilson (1972) for the CO_2 compensation point in F. arundinacea at 20–25 °C.

Values of $r_a^{CO_2}$, $r_l^{CO_2}$, and $r_m^{CO_2}$ are shown in Table 1 from which it can be seen that the wind-treated plants have lower stomatal but much higher mesophyll resistances than the controls. The magnitude of the mesophyll resistance, a residual term, is inversely related to the intercellular concentrations of CO_2; the use of a constant value of 55 µl/l being almost certainly an over-simplification justified in this case by the lack of appropriate data.

Young leaves of a tiller are frequently longitudinally folded and so r_a was measured before and after folding the model into a U shape. For comparative purposes the air flow rates through the cuvette have been converted on the upper axis of Figure 3 to wind speeds, these being estimated from a knowledge of the cross-sectional area of the cuvette and the rate of air flow through it. The form of the relationship between the boundary layer resistance and windspeed (Figure 3) is similar to that obtained by others, and the magnitude of r_a is greater than the values obtained by Landsberg and Ludlow (1970) for spruce needles and similar to those obtained by Thom (1968) for models of bean leaves. There is a small difference between the estimates

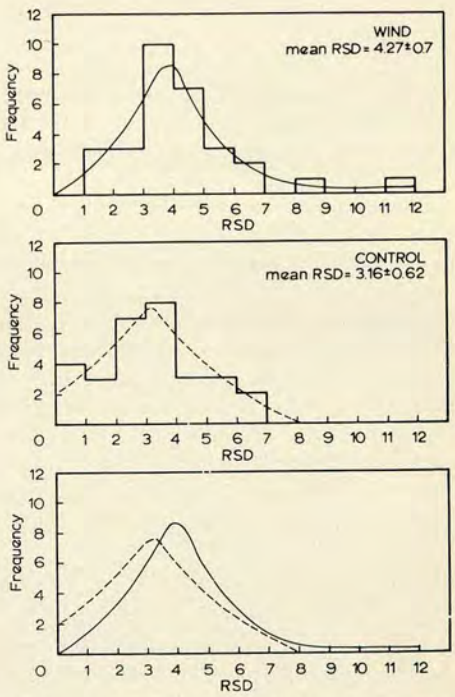

Figure 4. *Frequency distributions of relative saturation deficit* (RSD) *in control and wind-treated leaves of Festuca arundinacea.* The smoothed frequency distributions are combined in the lower part.

for folded leaves and those for flat ones, the latter being higher.

Figure 4 shows the water content, expressed as RSD of leaf populations in control and wind-treatment conditions. When the smoothed curves are superimposed there appears to be a difference between the two, but when compared using a t-test, the means differ only at the $p = 0.1$ level of significance.

Discussion

An assessment of the reasons for the lower rates of photosynthesis obtained during wind treatment should take into consideration that under such conditions grass blades knock and rub together, bend over and frequently rotate about their longitudinal axes. Such movements may produce permanent lateral fractures and necrosis of the leaf tips. It was once believed that mechanical shock, caused for example by attaching a porometer, led to stomatal closure (Knight 1916), although Williams (1949) in his re-consideration of this found the effect to be less than originally thought. The possibility of variation between species cannot however be neglected, and if the mechanical shocks due to wind did have a protracted stomatal closure effect in F. arundinacea this would be apparent from higher leaf resistance values. Our evidence of lower leaf resistance values (Table 1, Figure 3) would on the contrary suggest extra stomatal opening or lower cuticular resistance. Examination of the leaf surfaces of wind-treated plants using a scanning electron microscope has revealed small surface tears and signs of mechanical wear. If these effects are responsible for lower resistance one might expect this parameter to be highly variable because of the unique shock-history of each blade in the canopy, and indeed the wind-treated plants show a greater range of transpiration rates (Figure 2).

Reductions in assimilation rate of wind-treated plants have formerly been attributed to water deficits, and the data available suggest that leaf water deficit is proportional to the transpiration rate (Weatherley 1951, 1965). In the present experiment transpiration rate could not be measured in the wind-tunnel, but the measurements summarised in Figure 3 indicate that no difference in transpiration rate would result from boundary-layer effects since both the high and low (control) windspeeds were sufficiently high to result in minimal values for $r_a^{H_2O}$ of around 0.5 s cm^{-1}. Differences in transpiration rate in the tunnel would however arise due to the different leaf resistances, r_l, indicated in Table 1. These different transpiration rates would be small because of the high humidity and low temperatures used; the leaf/air water vapour pressure gradient is only 1.7 mbar. In view of this likely difference in the transpiration rate of the leaves we examined the leaf water content of a population of blades (Figure 4). The result indicates an overall small reduction in leaf water, but when the means are compared using a t-test they are significant only at the $p = 0.1$ level. The possibility should not be overlooked that a small average reduction in water content may mask quite large differences along the length of the blade.

Numerous experiments have been performed on the effect of leaf water content on photosynthesis. Unfortunately the interpretation of such experiments is complicated by stomatal closure; it is often not possible to distinguish between reductions in photosynthesis due to stomatal closure and those due to events in the mesophyll. In order to overcome this difficulty Slavík (1965) measured photosynthesis in stomata-less tissue in the form of liverwort thallus. In his experiments a 10 % reduction in water content was accompanied by a reduction in photosynthesis of about 10 %. Pisek and Winkler (1956) measured net photosynthesis and stomatal opening of leaves with varying water deficits. It is clear from their data, plotted and discussed by Gaastra (1963) that changes in photosynthesis occurred independently of stomatal resistance, since an increase in relative saturation deficit from 3 to only 5.8 % led to a 20 % reduction in photosynthesis even though the stomatal aperture was the same in each case. In barley a reduction in relative water content from 96.8 to 95.5 % led to decreases in levels of two different photosynthetic enzymes of 11 and 28.5 % (Huffaker *et al.* 1970). In addition to these observations of photosynthesis there are other observations on the effect of leaf water content on the components of mesophyll resistance. The intercellular space resistance, a function of the tortuosity of the spaces between the cells may be expected to depend on leaf water content (Jarvis 1971). Also, the cell wall component of the mesophyll resistance to water vapour transport depends on tissue water content (Fischer 1968). It is concluded from this brief review that quite small reductions in leaf water content may lead to reduced rates of photosynthesis, quite independently of the stomatal closure effect, and that the high mesophyll resistance we have found in the wind treated plants could well be due to their reduced leaf water content.

An advantage of the diffusion path analysis is that it enables one to predict the likely effect on overall CO_2 exchange of changes in various components of the diffusion pathway (Figure 5). It follows from Table 1 that the wind-blown plants behave quite differently in this respect to the controls. Small changes in the stomatal resistance in the control plants are likely to lead to large changes in photosynthesis because r_l is a large proportion of the total resistance. In the wind-treated plants this is not so. In both control and wind-treated plants r_a is a rather small component of the total resistance, and would be so in all but near-zero wind speeds where r_a rises sharply.

If we consider the transpiration process, in which only

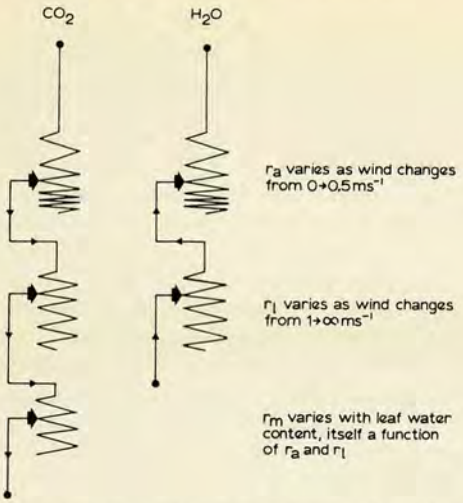

Figure 5. *Model of the effect of wind on CO_2 and H_2O diffusion pathways.*

r_a and r_l are involved, we see that r_a is a much larger proportion of the total resistance in both cases, so that changes in wind speed over the range indicated in Figure 3 are likely to lead to changes in r_a which would considerably influence transpiration rate. We might expect transpiration rate in the wind treated plants to be especially sensitive to wind speed over this low range because r_a is such a large component of $r_a + r_l$.

From an ecological viewpoint the idea of leaf resistance falling as a result of wind is important. Previously it has been thought that the effect of wind is merely to alter the boundary layer resistance. In many hill situations wind speeds are rarely operating over the range in which this resistance varies, and for most of the time the boundary layer resistance is likely to be uniformly low so that under these conditions the effect of wind on leaf resistance is likely to be crucial. The aerodynamic properties of leaves and the resistance of leaf surfaces to mechanical wear and abrasion may well be important factors in determining growth and survival.

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